Assessing changes in the agricultural productivity of upland systems in the light of peatland restoration

Volume 1 of 1

Submitted by Guy William Freeman, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, June 2017.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

(Signature) ……

Thesis abstract

Human activity has had a profound negative impact on the structure and function of the earth's ecosystems. However, with a growing awareness of the value of the services provided by intact ecosystems, restoration of degraded land is increasingly used as a means of reviving ecosystem function. Upland landscapes offer an excellent example of an environment heavily modified by human land use. Agriculture has been the key driver of ecosystem change, but as upland habitats such as peatlands can provide a number of highly valuable services, future change may focus on restoration in order to regain key ecosystem processes. However, as pastoral farming continues to dominate upland areas, ecosystem restoration has the potential to conflict with existing land use.

This thesis attempts to assess differences in the agricultural productivity of the different habitat types present in upland pastures. Past and present land use have shaped the distribution of different upland habitat types, and future changes associated with ecosystem restoration are likely to lead to further change in vegetation communities.

Three key contributors to agricultural productivity are examined. Firstly, variation in the nutritional quality of different upland habitats is assessed, in order to understand their value for grazing animals. Secondly, levels of livestock use in different habitats are compared in order to identify areas of particular importance for grazing. Finally, parasite populations are measured in different habitats in order provide an indication of which habitats pose the greatest potential risk of infection.It is shown that these factors appear to differ between habitats, meaning that agricultural productivity may show spatial variation in upland pastures. However, it appears that peatland restoration might have a negligible impact on farming in upland pastures due to apparent minor differences in the agricultural productivity of the habitats most likely to be affected.

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Author’s declaration

All the work within is the author’s own work, under the supervision of the named supervisors. Where the data of other people has been used this has been noted in the text.

Definitions

Abiotic: physical rather than biological; not derived from living organisms.

Acid grassland: grassland growing on acidic soils, such as those in moorlands and heathlands.

Agricultural improvement: intervention aimed at making land more suitable for agriculture.

***Agrostis*:** species of grass known as bents, characteristic of semi-improved upland pastures.

Alien: a species present outside of its natural geographic range.

Animal performance: factors which will decide the market value of an animal, such as milk production or weight gain.

Anthropogenic: originating in human activity.

Assemblage: all of the species within a particular habitat.

Biogeochemical cycle: a pathway by which a chemical substance moves through both the biotic and abiotic components of Earth.

Biotic: relating to living organisms.

Blanket bog: a peat-forming ombrotrophic mire.

Bryophyte: non-vascular plants, including mosses and liverworts.

Community: see Assemblage.

Definitive host: an organism supporting the sexually reproductive form of a parasite.

Dwarf-shrub: a short woody plant, typically referring to species in the Ericaceae (heather) family.

Ecosystem: a biological community of interacting organisms and their physical environment.

Ellenberg value: used to define the habitat preferences of plants based on abiotic variables.

Emerging disease: a disease whose geographic range or incidence is rapidly increasing.

Endemic disease: a persisting disease occurring within a specified area.

Eutrophication: excessive nutrient input in a water body.

Extensive: referring to farming systems with low levels of input and output relative to the land area being farmed.

***Festuca*:** species of grass known as fescues, characteristic of semi-improved upland pastures.

Forage: food such as grass or hay for grazing animals.

Graminoid: grass-like plants, including grasses, rushes and sedges/

Grazers: here refers to large grazing mammals, both wild and domesticated.

Herb: vascular plants other than graminoids, shrubs or trees.

Heterogeneous: varied in character.

Homogeneous: of the same kind.

Intermediate host: an organism supporting a non-reproductive form of a parasite.

Intensive: referring to farming systems with higher levels of input and output per unit of agricultural land area.

Invasion: the spread of an organism into an area where it was formerly absent.

***Juncus*:** here refers to the species soft rush *Juncus effusus,* unless stated otherwise.

Live weight-gain: the weight gained by an animal prior to slaughter.

Microhabitat: a habitat covering a limited extent, but differing from surrounding extensive habitats.

Minerotrophic: soils with higher nutrient levels and lower levels of acidity.

***Molinia*:** here refers to purple moor grass *Molinia caerulea,* a robust, tussock forming grass species characteristic of acidic soils.

Moorland: extensive areas of rough grassland or heathland.

***Nardus*:** the species mat grass *Nardus stricta,* a coarse, tussock-forming grass of dry acidic soils.

Ombrotrophic mire: a rain-fed, peat-forming wetland.

Overgrazing: damage to vegetation or soils due to high levels of grazing.

Palatable: a food which is favourable for consumption.

Paleoecological: the study of interactions between organisms across geologic timescales.

Palynological: analysis of plant pollen in soils or water bodies.

Parasite: an organism living in or on another organism, deriving nutrients at the other's expense.

Pasture: land used to graze animals.

Pathogen: a bacterium, virus or microorganism that can cause disease.

Peat: a soil type characterised by particularly high levels of organic matter.

Peatland: land consisting of peat soils or peat bogs.

Physiognomy: the form, structure or appearance of a vegetation community.

Questing: the behaviour of a tick when it is seeking a blood-meal.

Reclamation: the conversion of non-productive land for another purpose.

Regime shift: large, abrupt and persistent changes in the structure of an ecosystem.

Resilience: the ability of an ecosystem to absorb disturbances.

Rough grazing: grazing land which has not been cultivated.

Rush: here refers to soft rush *Juncus effusus,* a robust graminoid species.

Semi-improved: a habitat which has been improved, but not cultivated.

Semi-natural: an area modified by human activity but still retaining many natural features.

***Sphagnum*:** various species of bog moss important in the formation of peat in blanket bogs.

Succession: change in an ecological community over time.

Sward: an area predominantly covered by grass.

Trophic cascade: when loss of a predatory species from an ecosystem results in change at lower trophic levels.

Turbid: water which is cloudy or thick with suspended matter.

Upland: here refers to raised areas in England, Wales and Scotland with similar abiotic and biotic characteristics.

Vascular plant: plants containing lignified tissues allowing the transport of water and minerals.

Vector: an organism which transmits a disease or parasite from one animal or plant to another.

Chapter 1: Thesis introduction

1.1 Drivers of and response to ecosystem change

1.1.1 Background

The effect of environmental change on ecosystems has been well documented (Aber *et al.* 2001; Nelson *et al.* 2006; Halpern *et al.* 2008; Tylianakis *et al.* 2008; Borer *et al.* 2017). Current patterns of biodiversity are dictated by a complex interaction between numerous abiotic and biotic factors, and modifying any one of these factors has the potential to lead to ecosystem change (Figure 1). Change in ecosystems can be identified and measured by monitoring for change in any of their structural components, for example biodiversity change (Pereira & Cooper 2006; Butchart *et al.* 2010), or specific functions, such as primary production and decomposition (Hooper *et al.* 2012; Isbell *et al.* 2013).

Ecosystem structure comprises biotic factors, such as species composition, evenness and abundance, and abiotic factors, such as substrate composition, hydrology and soil chemistry. Environmental factors have long been used to explain the distribution and traits of species and assemblages (Gaston *et al.* 2008), with abiotic variables such as temperature and precipitation helping to predict the spatial occurrence of species (Sykes *et al.* 1996; Franklin 1998; Araujo & Guisan 2006;). When combined with biotic processes such as inter-species interaction, these factors can provide an accurate explanation of observed distributions of species and habitats (Araujo & Luoto 2007; Wisz *et al.* 2012). Ecosystem function is the sum of the processes in operation within an ecosystem. Function is determined by structure, with biotic components such as vegetation and soil microbial communities driving biotic and abiotic processes including evapotranspiration, carbon sequestration, water storage and nutrient cycling (Bosch & Hewlett 1982; Hobbie 1992; Post & Kwon 2000; Keim *et al.* 2006; Fang *et al.* 2007). Thus, the structure and function of an ecosystem are inextricably linked, with connectivity and feedbacks between abiotic functional processes and biotic structural components combining to define the characteristics of an ecosystem (Turnbull *et al.* 2010; Wainwright *et al.* 2011).

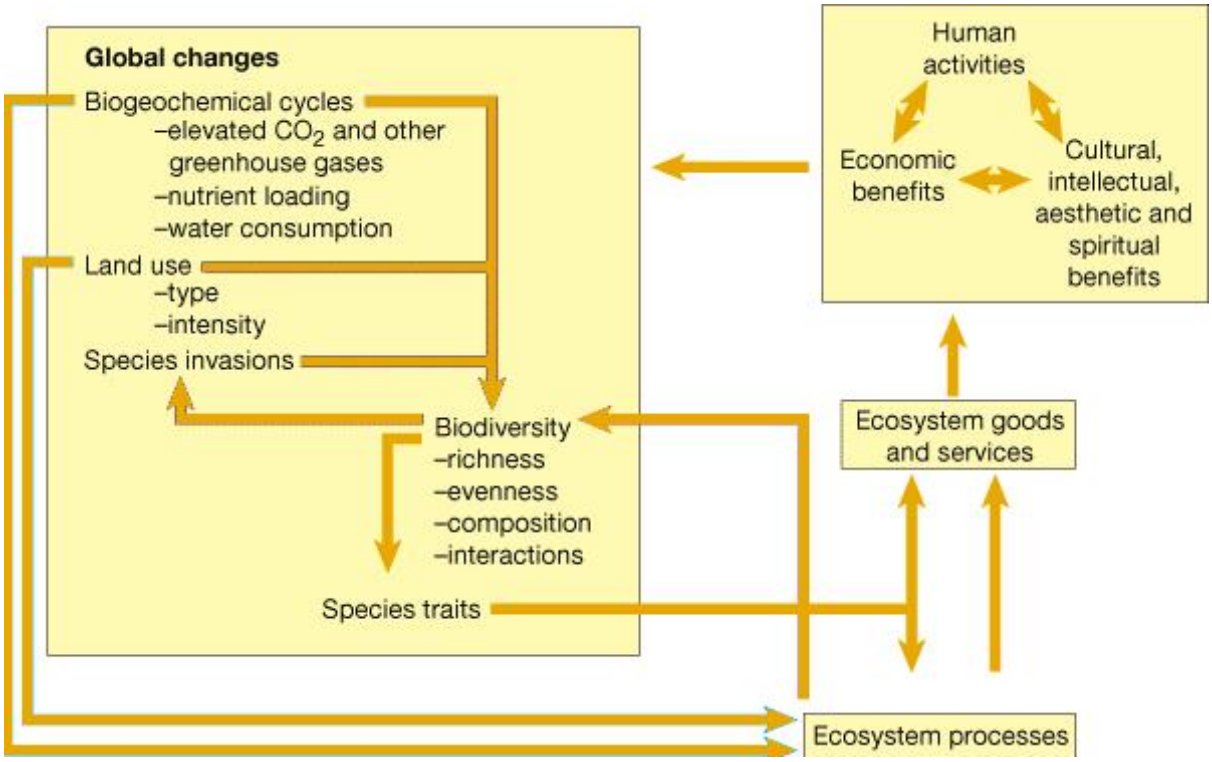


Figure 1: Diagram to show the interactions and feedbacks between human activity, biodiversity and ecosystem processes. Arrows indicate change. Adapted from Chapin III *et al.* 2000.

1.1.2 Natural drivers of ecosystem change

Ecosystems are dynamic, with natural disturbances driving changes in structure and function. An ecosystem's resilience refers to its ability to absorb such disturbances, and recover in the event of change (Gunderson 2000). All ecosystems are subject to natural environmental fluctuations and in some cases these may be extreme, such as the temporal variation in temperature in desert ecosystems (Holm & Edney 1973; Nobel 1984) and the daily changes in salinity and level of dissolved gases in intertidal rock pool ecosystems (Truchot & Duhamel-Jouve 1980; Morris & Taylor 1983).

Extreme natural disturbance events such as storms and flooding may have a dramatic effect on structure and function (Thom & Seidl 2016), but in the long term ecosystems are often resilient to such processes. Ecosystems may be adapted to high intensity natural disturbances such as fire, with the process driving change through succession and helping to increase or maintain

ecosystem function (Daubenmire 1968; Bond & Keeley 2005). After extreme disturbance, processes will gradually be reintroduced as species recolonise until the ecosystem returns to something resembling its former state through succession (Heinselman 1981). Biotic disturbances also have the potential to drive perturbations in ecosystem structure, such as when favourable conditions result in an overabundance of a particular species; however, these changes are often short-lived and cyclic, with species returning to their former, typical levels of abundance as resources are exhausted (Bengtsson *et al.* 2000).

While extreme events may have an immediate effect on community structure, if the ecosystem is suitably resilient it will return to its former state and there will be no long-term loss of function (Isbell *et al.* 2015), although this may depend on the extent to which abiotic functional processes and structural components are connected (Turnbull *et al.* 2008). Ecosystems with higher biodiversity and increased structural complexity are generally considered to be more resilient (Elmqvist *et al.* 2003). Where a community contains a number of species performing a similar function, the loss of one species will have a lesser impact as others will be available to occupy the same role and it is this functional redundancy of high biodiversity ecosystems which provides them with heightened ability to absorb disturbance (Loreau *et al.* 2001).

1.1.3 Human drivers of ecosystem change: global biogeochemical cycles

In contrast to the typically cyclic effect of natural perturbations, human-driven processes have far greater potential to cause long-term or permanent ecosystem change (Chapin III *et al.* 2000). If the biodiversity of an ecosystem is reduced it may result in a loss of resilience (Walker 1995; Peterson *et al.* 1998; Elmqvist *et al.* 2003;), and if the degraded ecosystem is subjected to further disturbance it may then pass a critical threshold at which a regime shift occurs (Folke *et al.* 2004). A regime shift is an abrupt change in an ecosystem to a radically different, stable state. Regime shifts have been observed in a number of ecosystems (Scheffer *et al.* 2001), for example, in freshwater lakes where eutrophication can drive a change from clear water plant communities to an algae-dominated turbid water state (Carpenter 2005), and in temperate reefs where rising oceanic temperatures associated with climate change result in a

switch from a kelp-dominated state to a characteristic tropical reef community (Wernberg *et al.* 2016). Certain ecosystems appear to be particularly prone to sudden changes in structure; for example, land degradation has been shown to result in a change from grassland to a shrub-dominated state in semi-arid ecosystems in a number of different regions (Rietkerk *et al.* 1996; Turnbull *et al.* 2008). Such changes in biological structure can lead to a fundamental change in ecosystem functionality, severely limiting the potential for regeneration of the former community. As a result, once a regime shift has occurred it is unlikely to be reversed without significant physical intervention, and in some cases it may be irreversible (Wilson & Agnew 1992; Carpenter *et al.* 1999).

Human activity drives change at a range of scales, and this has been a major cause of both recent and historical ecosystem change. At the global scale, human activity indirectly facilitates change through alteration of major biogeochemical cycles. Human activity has transformed global cycles of carbon, nitrogen and water (Vitousek *et al.* 1997a) and as the biotic components of ecosystems are heavily influenced by such abiotic inputs, changes in these cycles can result in changes in ecosystem structure and function.

The recent human-driven rise in the level of atmospheric CO_2 has been thoroughly documented (IPCC 2014), and the effects of this are recognised as a major threat to biodiversity and a key catalyst for ecosystem change (Walther *et al.* 2002; Parmesan 2006). The effects of rising temperatures, associated with higher atmospheric concentrations of CO_2, have been observed in ecosystems worldwide, driving shifts in the latitudinal distribution of polar ecosystems and the altitudinal range of montane ecosystems (Sturm *et al.* 2001; Perry *et al.* 2005; Parmesan 2006; Dirnbock *et al.* 2010). Additionally, rising temperatures may change ecosystems by altering the frequency and intensity of natural disturbances such as forest fire (Westerling *et al.* 2006). Higher levels of atmospheric CO_2 are also driving change through increased carbon deposition in terrestrial and aquatic ecosystems. For example, carbon uptake by oceans results in acidification, which acts synergistically with increased temperature to prevent the growth and recovery of coral reef ecosystems (Hughes *et al.* 2003). Higher CO_2 levels can also have a direct impact on the biotic component of ecosystems by affecting photosynthesis rates (Melillo *et al.* 1993), and as this response varies between plant species there is potential for change at the

ecosystem level through the alteration of a community's plant species composition (Taub 2010).

The global hydrological cycle has also been heavily affected by human activity, with large scale alteration of the flow, distribution and availability of water (Vorosmarty & Sahagian 2000). Hydrological factors make an important contribution to ecosystem structure and therefore changes in hydrology can act as a driver of ecosystem change, with aquatic, wetland and riparian habitats being affected particularly severely (Stromberg *et al.* 1996; Bunn & Arthington, 2002; Graf 2006).

Furthermore, the human driven increase in nitrogen fixation rates has had a major impact on the global nitrogen cycle, with an increase in nitrogen input into ecosystems resulting in eutrophication of freshwater and coastal habitats, loss of soil nutrients, and acidification of soils and waterbodies (Vitousek *et al.* 1997b). Nitrogen availability is a key determinant of vegetation community structure, and therefore alteration of this factor can leads to shifts in the species composition of an ecosystem (Bobbink *et al.* 2010).

Understanding the effect of changes in global processes on ecosystems is complicated by an intricate series of interactions and feedbacks between different biogeochemical cycles (Arneth *et al.* 2010). Climate change, driven by rising CO_2 levels, is expected to lead to an increased intensity of the hydrological cycle (Trenberth 1999), thereby potentially enhancing the effect of hydrological change on ecosystems. In addition, a feedback exists between the two processes, with climate change driving an increase in water vapour in the lower atmosphere (Held & Soden 2000) which subsequently amplifies the warming effect of increased CO_2 concentration and exacerbates the effect of climate change on biodiversity. In contrast, increased nitrogen deposition may contribute to alleviating the effects of climate change on ecosystems by promoting plant growth and thereby increasing carbon sequestration in vegetation and soil (Vitousek *et al.* 1997b).

1.1.4 Human drivers of ecosystem change: land modification

Human activity is also directly responsible for extensive and substantial modification of ecosystems through changes related to land use. Humans obtain numerous resources from ecosystems, but excessive exploitation of these resources may drive ecosystems to collapse (Jackson *et al.* 2001). Species do not contribute equally to ecosystem function, with those which are crucial to ecosystem functioning being known as keystone species. Large predators can act as keystone species, enforcing top down control over the abundance of species in lower trophic levels, and therefore trophic cascades may occur when these species are lost leading to dramatic changes in ecosystem structure (Daskalov 2002; Hebblewhite *et al.* 2005; Estes *et al.* 2011). Ecosystem engineers play a similarly important role by modifying their environment, often to the benefit of coexisting species, and therefore having a disproportionately large impact on ecosystem function. Trees in forest ecosystems act as engineers by providing refugia in the form of shed branches, and greatly increasing soil fertility with dropped leaves (Jones *et al.* 1994; Jones *et al.* 1997), and therefore their loss through deforestation may lead to the loss of numerous other species reliant on these processes.

The biota of an ecosystem may also be altered following biological invasion. Either intentionally or accidentally, humans have transported a wide range of species far outside of their natural ranges, and those species that are able to invade pose a threat to biodiversity through competition, predation and disease transmission (Mack *et al.* 2000; McGeoch *et al.* 2010).

While frequently affected by abiotic processes, shifts in the biotic components of ecosystems are also responsible for changes in abiotic processes and ecosystem functionality (Chapin III *et al.* 1997; Hooper *et al.* 2005) leading to a complex feedback loop between biodiversity and ecosystem processes. For example, deforestation can lead to changes in local hydrology (LeBlanc *et al.* 2008) and reduce soil stability leading to erosion (Zheng 2006). Alteration of ecosystem structure through species invasion may also affect ecosystem functioning by changing the frequency and intensity of natural disturbances such as fire (D'Antonio & Vitousek 1992; Mack & D'Antonio 1998).

Patterns of vegetation cover also play a role in regulating local climate (Stohlgren *et al.* 1998; Osborne *et al.* 2004), and can have implications at much larger scales. Global biogeochemical cycles may be affected by ecosystem

change, with forest ecosystems able to mitigate the effects of climate change through processes such as carbon sequestration and evapotranspiration (Bonan 2008; Canadell & Raupach 2008; Jackson *et al.* 2008). Soil communities may also play an important role in climate regulation. Where functioning properly, soils can sequester carbon (Lal 2004), whereas degradation through land use change may increase warming effects through the oxidation and release of stored carbon (Guo & Gifford 2002).

Although ecosystems have changed naturally over millions of years, the rate and extent of recent and present ecosystem change is unprecedented (Butchart *et al.* 2010; Pereira *et al.* 2012). Natural processes, such as volcanic eruption, can cause catastrophic ecosystem change, but human activity is the overriding driver behind modern ecosystem change. A huge proportion of the land surface has been directly modified by human activity (Sanderson *et al.* 2002) while virtually all ecosystems will have been affected to some extent by human activity. These changes have had a profound impact on global ecosystem function, with abiotic and biotic processes being affected at all scales (Vitousek *et al.* 1997; Ellis 2011).

1.1.5 Agriculture as a driver of ecosystem change

Among anthropogenic causes, agriculture is virtually unrivalled as a driver of ecosystem change, and its impact on ecosystems is set to continue with the increasing food demand of a rising human population (Matson *et al.* 1997; Green *et al.* 2005; Tilman *et al.* 2001). Attempts at agricultural improvement have involved interventions such as irrigation, drainage and fertilisation, all of which contribute to changes in abiotic processes (McLaughlin & Mineau 1995). Aside from the obvious modification of the habitat being improved, conversion of land for agriculture also affects surrounding ecosystems through changes in hydrology and nutrient loading (Stoate *et al.* 2009). A large area of the land surface is used for agriculture, with an estimated 25% occupied by grazing alone (Asner *et al.* 2004), and a large proportion of remaining ecosystems are either directly or indirectly affected by agricultural practices. Indeed, it has been estimated that the land area used for cultivation has increased by 466% between 1700 and 1980, with approximately 12 x 10^6 km^2 brought in to

cultivation over that period (Matson *et al.* 1997). The extent of this change has had a profound impact on biodiversity, with habitat degradation acting as a major driver of species loss (Foley *et al.* 2005; Reidsma *et al.* 2006). Conversion of land for agriculture continues, and practices have become increasingly intensive in order to meet human demand for food (Matson *et al.* 1997; Tilman 1999).

In the first instance, conversion for agriculture may lead to an immediate change to an ecosystem. For example, large areas currently used for agriculture were previously forested, with conversion requiring the clearance of native vegetation cover (Laurance *et al.* 2014), which may result in irreversible change in ecosystem function even if the land is subsequently left to revert to forest (Dupouey *et al.* 2002). Similarly, wetlands have been targeted for use in agriculture, with fertile soil and gentle terrain offering an incentive for conversion. However, in order to be brought in to use for agriculture extensive drainage is necessary, leading to a complete change in the characteristics of the ecosystem (Scanlon *et al.* 2007; Blann *et al.* 2009). Use of natural grasslands for pastoral farming may require less intensive modification, but management can affect processes such as soil erosion at a range of scales, with a subsequent impact on regional water quality (Bilotta *et al.*2007; Brazier *et al.* 2007; Peukert *et al.* 2014).

The impact of agricultural intensification on ecosystems can result in the loss of beneficial services (Tilman 1999; Dale & Polasky 2007). Loss of ecosystem services can lead to a negative feedback loop causing further damage and decreasing the potential for recovery; for example, once soil structure is damaged by ploughing there is a loss of nutrients through leaching, causing lower fertility and a reduced ability to accumulate additional nutrients (Diacono & Montemurro 2010). As ecosystem degradation causes a loss of functionality, external inputs are required in order to maintain the land for agriculture, with arable farming being heavily reliant on the addition of fertiliser to maintain crop yields (Erisman *et al.* 2016). Where agriculture is abandoned, the initial land conversion can still have a permanent effect on the soil chemistry and vegetation structure of regenerating ecosystems (Abrams & Hayes 2008; Yesilonis *et al.* 2016; Sohng *et al.* 2017). The presence of grazing animals can alter ecosystem characters both within and outside of a site (Bilotta *et al.* 2007),

and where overgrazing occurs there may be a permanent modification of soil structure, causing vegetation loss and leading to soil erosion which may result in desertification in extreme cases (D'Odorico *et al.* 2013).

Intact ecosystems may offer some degree of biological control of pest species, but conversion for agriculture simplifies ecosystem structure and may result in the loss of this service (Chaplin-Kramer & Kremen 2012; Lou *et al.* 2013). Again, removal of a natural process requires an artificial solution; in this case, the application of pesticides (Geiger *et al.* 2010). However, this affects populations of non-target organisms, modifying ecosystem structure with the potential to deplete services such as pollination (Potts *et al.* 2010) which are highly valuable to the agricultural industry (Gallai *et al.* 2009).

The effect on surrounding ecosystems may be significant (Stoate *et al.* 2009). Intensive agricultural landscapes are inhospitable to many species, and therefore they may reduce ecosystem functionality by reducing connectivity between populations of species living in favourable habitat patches (Hooftman & Bullock 2012). This isolation can result in a gradual erosion of biodiversity, leading to an associated reduction in certain ecosystem processes (Fischer & Lindenmayer 2007; Karp *et al.* 2012). Agriculture may also have a detrimental effect on proximal ecosystems by altering regional hydrology (Bilotta *et al.* 2007; Brazier *et al.* 2007; Scanlon *et al.* 2007). Arable farming relies heavily on extraction of water from local sources, which can threaten both aquatic and terrestrial ecosystems in the surrounding area (Terrado *et al.* 2016). Irrigation also alters ecosystem function on the land being farmed, driving changes in processes such as production and decomposition of organic matter (Arroita *et al.* 2013; Moinet *et al.* 2017). Furthermore, where rivers and streams are dammed, in order to provide a consistent water supply for irrigation of crops, regional hydrological processes may be altered. Changes in hydrology may lead to loss of wetland and riparian habitats, and a reduction in functionality of those which remain (Bunn & Arthington 2002; Gordon *et al.* 2008).

The increased input of nitrogen and phosphorus associated with agricultural intensification can also have a detrimental impact on freshwater and marine ecosystems through eutrophication (Tilman 1999). Furthermore, biodiversity may be affected through the medicinal treatment of livestock, which introduces chemicals that can be harmful to invertebrate dung communities (Lumaret &

Errouissi 2002; Floate 2006; Mann *et al.* 2015), thereby affecting the key ecosystem processes of decomposition and waste removal.

The extent to which agriculture alters ecosystems depends greatly on the type of farming system. Some studies have suggested that organic farming systems have a lesser impact on ecosystem processes and a reduced effect on surrounding habitats when compared to intensive agriculture (Maeder *et al.* 2002; Hole *et al.* 2005;). Furthermore, where farming does not require the direct conversion of land, such as in extensive, semi-natural systems, livestock grazing within an ecosystem may help to increase biodiversity and improve ecosystem function (van Wieren 1995; Luoto *et al.* 2003;). Such ecoagriculture systems have the potential to effectively combine farming with the conservation of biodiversity and the provision of ecosystem services (McNeely & Scherr 2001).

1.2 Ecosystem services

1.2.1 The value of ecosystem services

Increasingly, functioning ecosystems have been viewed in light of the benefits they can provide for people. It is recognised that humans are reliant on, or greatly benefit from, a wide range of goods and processes provided by ecosystems (Diaz *et al.* 2006; Guo *et al.* 2010).

The Millennium Ecosystem Assessment, commissioned by the United Nations to assess the effect of ecosystem change on human well-being, divides ecosystem services into four categories: provisioning services, regulatory services, supporting services and cultural services (2003). Provisioning services relate to actual goods that can be obtained from ecosystems, such as food and raw materials. Regulatory services are those that act to control the impact of environmental perturbations such as flooding or disease. Supporting services do not directly affect humans, but are processes such as pollination and nutrient cycling that are required to obtain the benefits of other ecosystem services. Cultural services provide benefits in areas such as recreation and general mental wellbeing. While it is difficult to measure the monetary value of these ecosystem services, the economic contribution is estimated to be in the trillions

of dollars per year (Costanza *et al.* 2014). With a growing human population imposing increasing pressure on landscapes, ecosystem services provide a strong economic argument for the preservation and restoration of habitats (Daily *et al.* 2000; Balmford *et al.* 2002).

The benefits of provisioning services are obvious, as goods such as drinking water from rivers, timber from forests, and fish from oceans meet immediate human needs and are easily quantifiable. In contrast, the benefits of regulatory and supporting services are harder to value (Costanza *et al.* 1997) and have often been overlooked as a result. However, with a growing awareness of the crucial contribution regulatory and supporting services make to human society, it is increasingly recognised that functioning ecosystems can have value to humans without providing material goods.

Ecosystems provide a varied array of services to humans, with crucial regulatory services include atmospheric gas regulation, climate regulation, disturbance regulation and water regulation. Photosynthesis plays a key role in atmospheric gas regulation, and aside from the obvious O_2 production, its carbon fixation has the potential to mitigate the impacts of climate change (Stenger *et al.* 2009). Climate change poses numerous problems for humans, and large sums are spent on technological solutions to try and alleviate future impacts, but forest ecosystems are likely already playing a key role in climate change mitigation through accumulation of carbon (Bonan 2008; Pan *et al.* 2011).

Similarly, ecosystems can assist with the regulation of water supplies, and as a growing human population is putting increasing pressure on water sources reliability of supply is an important issue. As an increasingly intense hydrological cycle is to be expected with warming (Trenberth 1999), any contribution of ecosystems to climate change mitigation should help to reduce the intensity of precipitation patterns and thereby increase the consistency of water supply. In addition, habitats such as forest alter groundwater flow through water extraction and storage reducing the intensity of storm flow events (Huang *et al.* 2003; van Dijk & Keenan 2007) to the benefit of those industries such as hydroelectric power which are reliant on a stable flow (Guo *et al.* 2000).

Ecosystems may contribute to disturbance regulation by dampening the effects of natural perturbations, as with the previously mentioned flood storm flow reduction provided by intact forest. They can also reduce the impact of environmental disturbances through physical protection; for example, ecosystems such as sand dunes, mangroves and saltmarshes can play a vital role in reducing the impact of storm surges and coastal erosion on settlements (Borsje *et al.* 2011; Gedan *et al.* 2011).

Loss of ecosystem functionality can increase the risk and severity of biotic disturbances such as disease outbreak (Patz *et al.* 2000). In addition to threatening human health, disease has a huge impact on industries such as agriculture, affecting livestock and crops and thereby reducing food availability and economic yields (Anderson *et al.* 2004; Purse *et al.* 2005; Babiuk *et al.* 2008). It has been demonstrated that a number of emerging diseases thrive in heavily degraded landscapes (Patz *et al.* 2004; Sutherst 2004), whereas intact, functioning ecosystems may provide a biological buffer against outbreaks, as greater biodiversity provides a wider range of potential host species, thereby producing a 'dilution effect' in which infection rates in humans may decrease (Civitello *et al.* 2015). Furthermore, the presence of structurally complex ecosystems in the proximity of arable land can impose a biological control on pest numbers, reducing the impact on industry (Bommarco *et al.* 2013).

Supporting services are integral to the proper functioning of provisioning and regulatory ecosystem services. For example, functioning wetland and forest ecosystems can help to improve water quality by reducing runoff of sediment and accumulating contaminants, thus playing a vital role in the provision of clean water required for drinking and the functioning of aquaculture industries (Brauman *et al.* 2007). Nutrient cycling is another valuable supporting service, with increased diversity in soil communities leading to increased stability and improved nutrient and water use efficiency (Brussaard *et al.* 2007), and thus improving growing conditions for arable farming. Aside from the value to agriculture, nutrient cycling is an important component of ecosystem function, meaning that many regulatory or provisioning services would be depleted without this supporting service.

Pollination provides a similar example of a service that is not only valuable to industry (Klein *et al.* 2007), but also highly important to ecosystem function as a

whole. Diversity and abundance of pollinators is greater in structurally complex, intact ecosystems, and therefore ecosystem simplification associated with habitat degradation may reduce the ability of ecosystems to perform this service (Kremen *et al.* 2002; Connelly *et al.* 2015; Nicholson *et al.* 2017).

Ecosystem change affects the ability of ecosystems to provide services by altering their functionality. While provision of goods is an extremely important service, overexploitation of a particular ecosystem component may lead to a change in structure and the loss of valuable ecosystem processes. When ecosystem structure is altered through habitat degradation or resource exploitation, there is potential for valuable regulatory and supporting ecosystem services to be lost (Foley *et al.* 2005). For example, deforestation dramatically modifies ecosystem structure and results in the reduction or loss of services such as nutrient cycling, pollination, and water regulation (Nasi *et al.* 2002). While all ecosystems function to some extent, greater structural complexity typically produces a wider range of ecosystem processes, and therefore intact habitats show increased functionality over degraded habitats and have greater value in terms of ecosystem service provision (Isbell *et al.* 2011).

1.2.2 Restoration ecology

Although human activity has been a major driver of ecosystem change (Vitousek *et al.* 1997), a greater understanding of the benefits provided by properly functioning ecosystems has led to increasing efforts to revert ecosystems to an intact state for the services they can provide (Aronson *et al.* 2006). Thus, although the overwhelming majority of global ecosystem change is reducing functionality, efforts are being made to redress the balance. Restoration ecology is a relatively new field, focussed on the restoration of degraded habitats to increase biodiversity and ecosystem functionality. Recognition of the importance of ecosystem services has seen the emergence of large-scale global schemes, such as The Restoration Initiative (TRI) from the International Union for Conservation of Nature (IUCN) which is aiming to restore 150 million hectares of degraded land to forest by 2020 (IUCN 2016).

The effort required, and likelihood of success, for ecosystem restoration varies greatly depending on situation (Hobbs & Cramer, 2008). Those which are only

slightly degraded, or are highly resilient, may revert to their former state through natural regeneration with no human input required. In contrast, heavily degraded ecosystems and those which are less resilient are likely to require major physical intervention to return to their former condition.

Due to the complexity of ecosystem structure and processes, restoration is challenging. Indeed, analysis of restoration projects suggest that a relatively small proportion succeed in increasing biodiversity or provision of ecosystem services, and restored ecosystems lack the functionality of reference, intact ecosystems (Benayas *et al.* 2009). This reduced functionality means that the economic value of services from restored ecosystems is often considerably lower than those in pristine ecosystems (Bullock *et al.* 2011). Success appears to differ greatly depending on the ecosystem being restored; for example, restoration of terrestrial tropical ecosystems yields significantly greater improvements in biodiversity and ecosystem services than restoration of terrestrial temperate ecosystems (Benayas *et al.* 2009). Supporting services also appear to be easier to regain than regulatory services, but restoration of both may be possible depending on the scale of the restoration project and the extent of ecosystem degradation (Benayas *et al.* 2009).

Ecosystem restoration often focuses on an end-goal of improving biodiversity with the assumption that this will increase ecosystem service provision. However, the link between biodiversity and ecosystem service restoration is complex with these two measures of success often showing differing trends following restoration (Mace *et al.* 2013). Furthermore, the restoration of biodiversity to a previous level is not always necessary to facilitate restoration of services, with the potential for a smaller number of species, or a replacement non-native species to perform a similar function (Bullock *et al.* 2011).

Ecosystem restoration projects can set unrealistic targets, resulting in a perception of failure; however, despite the variability in success rate, restoration offers an improvement in functionality over taking no action at all, and due to the extensive degradation of ecosystems worldwide it is often the only option available (Hilderbrand *et al.* 2005). While there may be uncertainty surrounding the outcome of any individual restoration project, some have successfully managed to restore a level of function to degraded ecosystems, allowing the recovery of ecosystem services (Jenkins *et al.* 2010; Koch & Hobbs 2007).

Restoration is frequently suggested to be a means of reviving ecosystem services in degraded landscapes. Research into the effectiveness of restoring pollination services is lacking, but it has been suggested that recovery of native bee populations may be an effective means of improving pollination services in agricultural systems (Kremen *et al.* 2002). Similarly, recovery of biodiversity has been suggested as a way of facilitating water quality improvement, as with the reestablishment of bivalve communities in estuaries to reduce coastal eutrophication and water turbidity (Nakamura & Kerciku, 2000).

Restoration can play a role in the recovery of regulatory services. Disturbance regulation services may be restored through landscape change; for example recovery of functioning wetlands can help to reduce flood risk in populated areas (Zedler & Kercher 2005). Restoration of biodiversity may also act to mitigate environmental disturbances, with the recovery of populations of apex predators suggested as a method of reducing incidence of vector-borne disease (Pongsiri *et al.* 2009). When enacted over a suitable scale, restoration projects may allow the return of regulatory services over large areas, as in the Chinese GTGP initiative which has turned a large area of degraded land from a carbon source to a sink through recovery of vegetation cover and an associated increase in carbon sequestration (Feng *et al.* 2013).

1.3 Ecosystem change in uplands

1.3.1 Landscape change in UK uplands

The categorisation of uplands is imprecise, but it often refers to land above the upper altitudinal limit of cultivation (King 1977). However, defining upland areas on altitude alone ignores the fact that characteristic upland habitats occur on lower ground at higher latitudes, with vegetation of upland character present at sea level in northern and western parts of Scotland (Averis *et al.* 2004). Therefore, a broader categorisation is frequently used based on vegetation type, encompassing raised areas of England and Wales, and large parts of Scotland (Figure 2). For agriculture, the most relevant definition of ‘uplands’ is the land that is recognised by the EU as ‘Less Favoured Areas’; areas where the abandonment of agriculture is a persistent threat owing to factors such as

poor productivity, and a small human population that is predominantly dependent on agricultural activity (EC 2017). In the UK, uplands are distributed in western and northern parts, ranging from Cornwall to far northern Scotland. While upland areas are widely separated, they share many characteristics. Typically the terrain is rough, with hilltop plateaus and valley bottoms being separated by steep slopes and rocky outcrops. Climatic conditions are harsh, with higher precipitation and lower mean temperatures than surrounding lowlands.

All British uplands have been modified by human activity. Until roughly 5000-6000 years ago, all but the highest peaks had extensive tree cover (Averis *et al.* 2004). The current open character of upland landscapes is mainly manmade, through deforestation, with such habitats only occurring naturally in the few areas that rise above the tree line (King 1977). Tree removal has had a profound effect on the structure and function of upland ecosystems, with the current observed pattern of semi-natural habitats relating directly to human land uses over the past few thousand years (Miles 1987).

Originally, many trees were removed for use as fuel, although conversion of land for agriculture later became an important driver (Reed *et al.* 2009). The loss of tree cover will inevitably have had a major effect on upland ecosystem processes, with a reduction in soil stability and a lack of nutrient input from shed leaves and decaying branches leading to low-quality, infertile soils (Copeman 1978; King 1977). Furthermore, as upland tree cover reduces runoff (Harding 1978; Marshall *et al.* 2009), water cycling and storage processes are likely to have decreased with the loss of intact forest. Without human intervention, there is limited potential for recovery of upland forest in the short-term. Harsh climatic conditions and poor soil quality mean that rates of regeneration are slow, and to compound the problem seedlings rarely have the opportunity to settle without being grazed (Clutton-Brock *et al.* 2004).

In the time since deforestation, agriculture has continued to be the key driver of change in upland ecosystems. A large part of agriculture-driven change in the uplands has been due to efforts to improve the land for farming (Holden *et al.* 2007). A variety of techniques have been employed in order to improve the

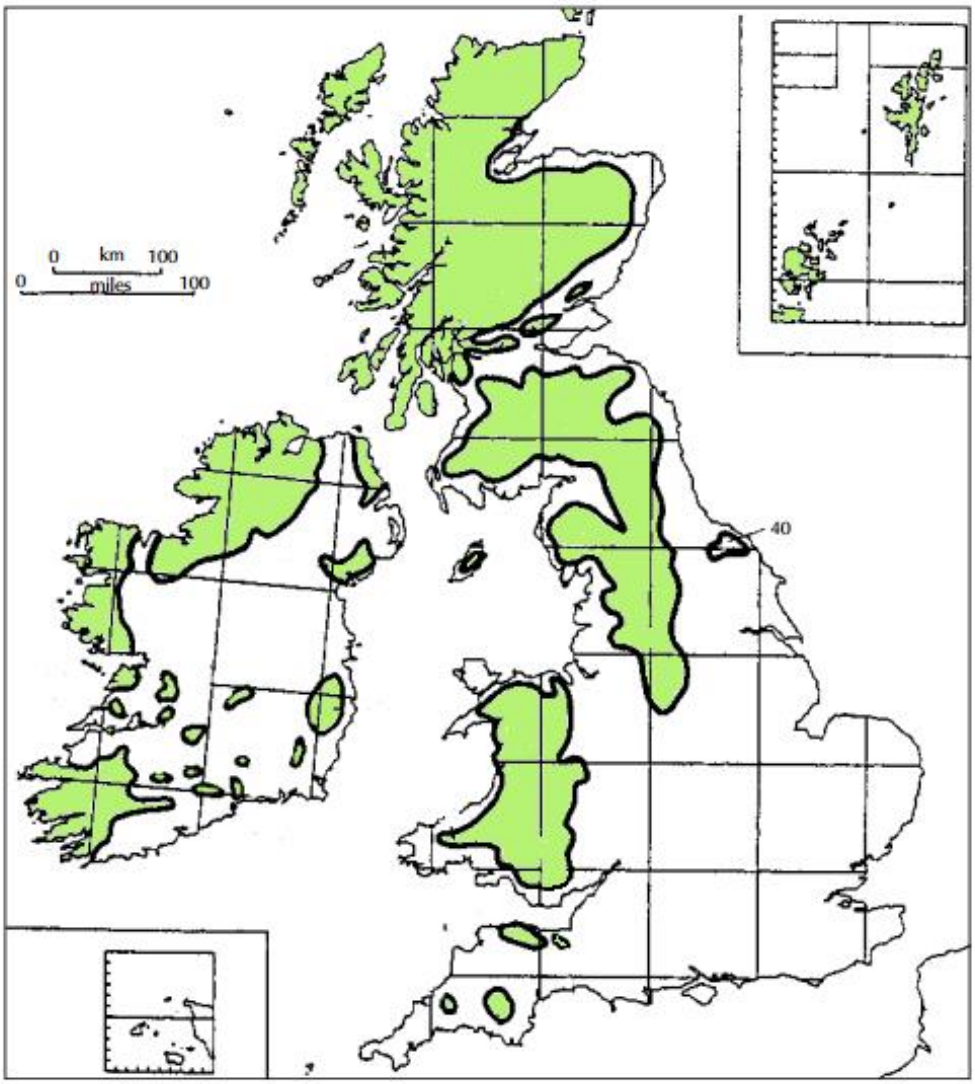


Figure 2: Map of the British Isles with upland areas highlighted in green. Adapted from Averis *et al.* 2004.

grazing value of upland pastures; drainage ditches were cut into areas of blanket bog in order to reduce wetness and make them suitable for grazing, while rough moorland was subjected to techniques such as ploughing, burning, and the addition of lime and nitrogen to improve fertility (Copeman 1978; King 1977; Maltby 1995). These processes have had a substantial impact on soil structure and chemistry, and the current fine-scale distribution of different moorland vegetation types is heavily affected by previous attempts at land conversion (Miles 1987).

Despite the considerable effort expended on reclaiming upland pastures, it is questionable how effective these techniques have been in improving land for agriculture (Wilson *et al.* 2011). The potential for arable farming is extremely limited, due to short growing seasons and difficulties in harvesting (Copeman

1978; Eadie & Smith 1978). Pastoral farming has been considerably more successful, but hill farms still face numerous challenges in trying to remain economically viable (Jones 1978; Reed *et al.* 2009). Due to unproductive pastures, stocking densities are low by necessity, reducing yields and leading to a requirement for extensive areas of land for the production of a relatively small number of animals (King 1977). The productivity of upland pastures may also suffer due to reduced livestock health. Stock grazing extensive pastures will come in to contact with wild animals which may act as reservoirs for disease (Gilbert 2016; Jeffries *et al.* 2014). Furthermore, impoverished soils may result in nutrient deficiencies in grazing animals, resulting in health disorders (Lidiard 1995). Low productivity means that disease outbreaks, such as the 2001 foot and mouth epidemic, can be particularly devastating (Franks, 2003).

As mentioned, it is issues such as these which have led to the designation of hill farming regions as Less Favoured Areas (LFA) by the government's Food and Environmental Research Agency (FERA), allowing struggling farmers to qualify for financial support (FERA 2015). In the mid-1900s stocking densities in uplands began to decrease due to diminishing financial returns, before the introduction of subsidies led to a resurgence in hill farming. Indeed, as payments were made per head of livestock stocking densities were increased to unsustainably high levels (Winter *et al.* 1998), leading to overgrazing and destruction of vegetation and soil communities. This overstocking has driven change in uplands, accelerating losses of biodiversity and affecting ecosystem processes, both in uplands and in surrounding lowlands (Sansom 1999).

Agriculture is not the sole driver of ecosystem change in uplands. As hill farms have struggled commercial forestry has become more frequent, resulting in the afforestation of large areas of UK uplands (Mount *et al.* 2005). This typically involves the planting of dense monocultures of non-native pines, which prevent the development of native vegetation communities (Wallace *et al.* 1992). These plantations may increase the acidity of surrounding ecosystems during establishment and after harvesting (Puhr *et al.* 2000; Reynolds & Stevens 1998).

In addition, recreational activities have made a contribution towards shaping upland landscapes. For example, burning of moorland for grouse shooting is responsible for the maintenance of large tracts of heather in upland areas

(Holden *et al.* 2007; Worrall *et al.* 2007). Human activity can also influence upland ecosystems indirectly. Sulphur deposition associated with increased industrial activity has led to acidification of aquatic and terrestrial upland habitats, leading to changes in their species composition (Woodin & Farmer 1993). Furthermore, changes in the nitrogen cycle have led to increased deposition of atmospheric nitrogen in upland areas, which is thought to contribute to the loss of *Sphagnum* mosses and the invasion of the grass *Molinia caerulea* in degraded mire systems (Tomassen *et al.* 2003).

Upland ecosystems can provide a number of important services, such as carbon sequestration, water regulation, and nutrient cycling (Bonn *et al.* 2008; Reed *et al.* 2009; Grand-Clement *et al.* 2013; Curtis *et al.* 2014). However, their extensive modification has seen an erosion of ecosystem function, with a large proportion of protected areas in uplands considered to be in unfavourable condition at present (Williams 2006). Restoration of uplands is complicated by the differing goals of different projects, with a lack of consensus on whether uplands should be returned to their historic, forested state, or whether restoration should aim for the simpler target of vegetation recovery while maintaining the familiar open character of the landscape (Carver 2007). Future decisions have major implications for hill farming systems, with some conservation targets requiring the cessation of agriculture, and others requiring grazing as a management technique. There is thus a need for cooperation and discussion between a variety of stakeholders in order to form a sustainable future for upland environments.

1.3.2 Peatlands

Peat soils are formed under saturated, anaerobic conditions and are recognised by a particularly high proportion, ranging from 30–100%, of organic matter (Lindsay 2010). Peat can be divided into layers, with the deeper catotelm layer being more compact, receiving decreased oxygen penetration and showing lower water conductivity. The active acrotelm surface layer is where the majority of peat formation occurs, with foliage of mire species decomposing over protracted periods to form the typical highly organic soil (Lindsay 2010). Peat formation can occur in a variety of wetland types, but in the UK the majority of

peat accumulation occurs in blanket bog, a habitat restricted to high precipitation areas of the western and northern uplands (Maddock 2008). Within these upland areas, blanket peat is estimated to cover approximately 1.5 million hectares (BRIG 2008). Blanket bog is a form of ombrotrophic mire, obtaining water purely from precipitation rather than from flushes or streams. Peat deposition requires an active vegetation layer in order to provide organic matter for decomposition. In the UK, pristine blanket bog contains a characteristic suite of species with subtle variations associated with geography (BRIG 2008). *Sphagnum* moss is particularly important for peat accumulation, while cotton grass (*Eriophorum* spp.) is also a common component of peat soils (Lindsay 2010).

Peatlands in the UK and elsewhere have seen extensive damage from human activity. One of the most harmful processes has been drainage, carried out with the aim of improving the land for grazing or forestry (Holden *et al.* 2004; Haigh 2006). The harvesting of peat for use as fuel, or in the horticulture industry, has also seen the degradation of large areas of peatland (Alexander *et al.* 2008). Human-driven changes in the hydrology of peatland results in change in vegetation communities, and an alteration or loss of ecosystem processes (Ramchunder *et al.* 2009). Peatlands have also been harmed by changes in biogeochemical processes, such as increased nitrogen deposition, which have a detrimental impact on important bog species (Hogg *et al.* 1995; Tomassen *et al.* 2003). As a result, the extent of pristine peatland has been dramatically reduced, with the IUCN peatland program estimating that a maximum of 20% of peatlands in the UK exist in an undamaged state (Bain *et al.* 2011). Degraded peatlands may occur in a variety of forms. Degrading processes often result in the replacement of characteristic mire species with those favouring drier conditions due to a lowering of the water table (Ramchunder *et al.* 2009; Gatis *et al.* 2015;Swindles *et al.* 2016), but in cases where a bare peat layer has been exposed through removal of vegetation, rapid soil erosion may prevent re-colonisation of plants leading to the persistence of a barren, exposed peat surface (Bragg & Tallis 2001).

Intact peatlands are able to provide a variety of ecosystem services that degraded peatlands cannot (Parry *et al.* 2014). Importantly, it has been suggested that they may contribute to climate change mitigation. Due to their

accumulation of organic matter through protracted and partial decomposition, peatlands act as major carbon stores (Roulet 2000). Carbon flux on peatlands is highly variable (Gatis *et al.* 2015), but continued peat accumulation in active peatlands results in carbon sequestration, meaning that active peatlands have the potential to act as carbon sinks (Billett *et al.* 2010). The contribution of peatlands to climate change mitigation is countered by their emissions of other greenhouse gases such as methane, and their greenhouse gas balance shows significant temporal and spatial variability (Koehler *et al.* 2010). However, maintenance of intact peatlands remains highly valuable due to the large quantities of carbon stored within their layers, estimated at 584.4 megatonnes in English peatlands alone (Natural England 2010). Where peat is degraded through drainage there can be a significant release of CO_2 due to oxidation of the soil (Waddington & McNeil, 2002).

The impact of peatland rewetting on local hydrology has produced varying results, with the effects heavily dependent on factors such as the slope and fine-scale topography of a site, and preceding weather conditions (Grand-Clement *et al.* 2014; Luscombe *et al.* 2016). Even after restoration has been completed for many years, rewetted peatlands may not regain the full function of pristine blanket bog (Holden *et al.* 2011). However, in terms of ecosystem service provision, intact blanket bog generally appears to offer an improvement over degraded peatland (Haigh 2006). When compared to degraded peat soils, active peatlands may show reduced runoff as the vegetated layer acts to diffuse surface water flow, thereby delaying discharge into waterbodies downstream and protecting against the impact of storm events (Bragg 2002). Furthermore, where drainage ditches are present in degraded peatland, they may lead to flashier flow regimes following rainfall events, with shorter lag times and larger peaks (Robinson 1986; Holden *et al.* 2006). The reduction in surface water flow, and improved soil stability of vegetated peatlands may also contribute to improvements in water quality downstream due to a decrease in sediment runoff and loss of dissolved organic carbon (Holden 2005; Armstrong *et al.* 2010; Luscombe *et al.* 2016).

Increased understanding of the ecosystem services provided by intact peatlands has seen the emergence of a number of initiatives aimed at restoring degraded peatland areas to their former state (Vasander *et al.* 2003). In

particular, the role of peatlands in climate change mitigation has drawn attention from organisations such as the IUCN, whose peatland programme aims to restore one million hectares of upland peatland by 2020 (Bain *et al.* 2011). Restoration of peatland typically revolves around efforts to recover hydrological function through the physical blocking of drainage ditches (Armstrong *et al.* 2009; Grand-Clement *et al.* 2015). In theory, this will lead to pooling of water which will rewet the surrounding degraded peat, allowing recolonization of bog vegetation and formation of an active, peat accumulating surface layer. Studies have produced mixed results on the success of rewetting in restoring previous functionality, but there have been indications that in some situations the technique can revive carbon sequestration and water regulation processes (Wilson *et al.* 2010; Waddington & Price 2013).

1.4 Thesis outline

Uplands provide an excellent study system for examining the interaction between human land use and ecosystem change. Agriculture has had a profound impact on the current upland landscape, with an effect on the structure and function of upland ecosystems. However, due to the low productivity and limited potential for improvement of upland pastures, present-day hills farms could be particularly vulnerable to future ecosystem change. Ecosystem change can drive changes in vegetation communities, which could potentially affect the productivity of grazing systems. Furthermore, changes in ecosystem structure may affect disease risk by increasing or decreasing habitat suitability for vectors and parasites. As the distribution of different vegetation types is dictated by a combination of abiotic and biotic variables and past human land use, there is potential for large scale change if any of these factors are altered. With increasing understanding of the importance of restoring ecosystems for the services they can provide, uplands may see extensive change in future due to the valuable habitats they support.

While the effect of agriculture on upland landscapes is widely recognised, the potential for ecosystem change to affect upland farming systems remains understudied. This thesis aims to identify differences in the agricultural productivity of upland habitats in order to predict the way in which habitat

change, such as that caused by peatland restoration, might affect productivity. In order to examine differences between habitats, three factors, all of which could affect the productivity of a site, were measured:

1. Nutritional quality: the distribution of different vegetation communities is dictated by environmental variables such as the availability of nutrients, light, and water. As a result, vegetation is highly responsive to environmental change, and alteration of abiotic processes may lead to shifts in the structure and composition of plant communities. As upland areas typically suffer problems of low productivity, any change in the distribution of different vegetation communities could have an impact on the grazing value of a pasture. This study aims to determine whether different upland vegetation communities differ in their nutritional quality, in order to predict the way in which habitat change might affect the nutritional quality of upland pastures. In order to estimate the nutritional quality of different upland vegetation communities, the quality of individual upland plant species will be measured and used to estimate the quality of different habitats based on the prevalence of these species.

2. Livestock habitat use: food availability and quality influences the distribution of grazing animals, and therefore there is potential for ecosystem change to alter their distribution. As a result, grazing suitability could be altered if the prevalence of different habitat types changes. Furthermore, while stocking rates in uplands are generally low, where animals aggregate in favourable areas habitat degradation could occur. This study aims to determine whether different upland habitat types differ in their levels of use by grazing cattle, so that the effect of habitat change on the distribution of cattle in upland pastures, and the suitability of upland pastures for cattle, can be determined. In order to identify differences in habitat use by cattle, the density of cattle dung in different habitats is recorded, and timelapse cameras are used to monitor cattle visits to different parts of the study sites.

3. Parasite populations: by modifying habitats, changes in land use can affect the population density of parasites, which could potentially alter the risk of disease transmission in an area. Furthermore, agriculture may affect populations of parasites and blood-feeding vectors by providing a concentration of potential hosts, in the form of livestock As different vectors have different habitat preferences, ecosystem change could potentially affect disease risk by

altering the distribution of different vegetation communities in upland pastures. As upland farming systems are relatively unproductive, a change in parasite abundance could have an impact on sustainability. This study aims to determine differences in tick density in different upland vegetation types, in order to predict the areas of a site in which grazing animals are at greatest risk of coming into contact with ticks. Furthermore, this study attempted to establish the distribution of the intermediate host of liver fluke, *Galba truncatula*, on upland pastures, in order to identify the habitats in which livestock are at greatest risk of infection by fluke.

Chapter 2: Site descriptions and habitat mapping

2.1 Exmoor

2.1.1 Exmoor National Park

Exmoor National Park is situated in South West England, split between the counties of Devon and Somerset and covering an area of 692 km^2 (Figure 3). The area was designated as a National Park in 1954, with the original boundary remaining virtually unchanged since then (Wilson 1977). The majority of the park is comprised of an upland plateau, reaching 519 metres above sea level (a.s.l.) at its highest point. The northern boundary is coastal, with the terrain varying from high, steep cliffs to lowland plains. Rocks of the plateau are of Devonian age, and this platform is believed to have formed after tectonic activity raised it above surrounding land (Straw 1995).

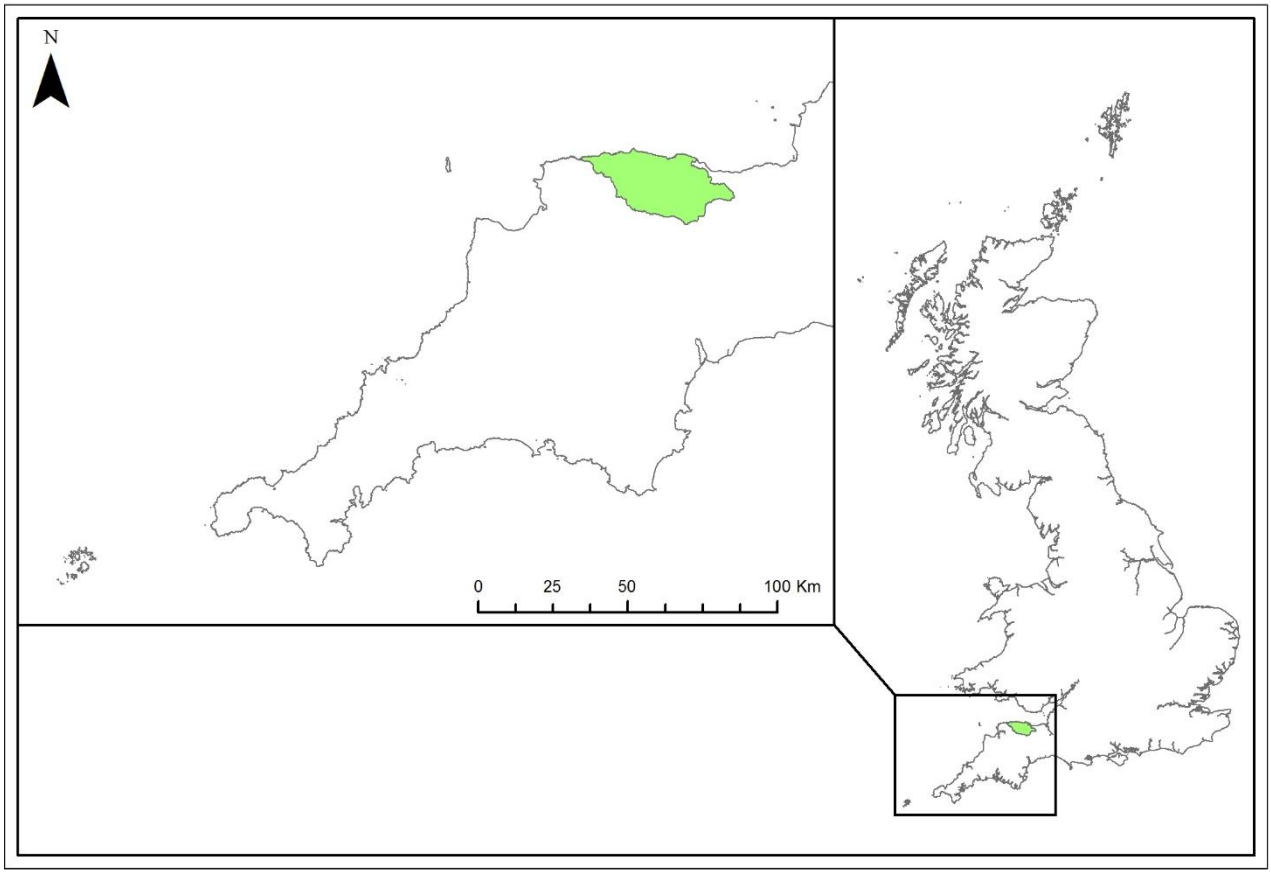


Figure 3: Map to show the location of Exmoor National Park (highlighted in green) within Great Britain.

A variety of rock groups exist within the park, but Old Red Sandstone is dominant. This relatively soft rock means that Exmoor is gently sloped, lacking the steep rocky outcrops characteristic of many other upland areas. The largest rivers are the Barle and Exe, which converge just outside of the national park boundary and drain a large part of the moor. Soils are acidic, with peat formation in waterlogged areas and brown earth soils on the better drained slopes (Maltby 1995).

Exmoor has a mean annual rainfall of 1800-2600 mm, and an average maximum daily temperature of 10-12°C (Met Office 2016). The elevation of Exmoor means that its climate is harsher than that of the surrounding lowlands, with higher precipitation and lower average temperatures. However, Exmoor is one of the southernmost of the UK's uplands, and therefore has a more favourable climate than the upland areas of Wales, northern England and Scotland. The warmer climate means that Exmoor's growing season can be over 50 days longer than in areas of similar altitude in Scotland (Miller *et al.* 1984).

2.1.2 Landscape change on Exmoor

At the last glacial maximum, ice cover stopped just north of Exmoor. During this period, the dominant habitat would have been similar to that of present day Arctic tundra, but glacial retreat led to a change in vegetation (Maltby 1995). Increasingly favourable climatic conditions led to colonisation by trees around 8000 years B.P., with birch and pine in the higher altitude areas and broadleaved woodland on lower slopes (Essex 1995). Palynological analysis from peat cores indicates that up until approximately 1500 years ago Exmoor still had large areas of forest cover (Merryfield & Moore 1974). However, with human settlement tree cover was gradually eroded and clearance was likely to have been virtually complete by the late Bronze, or Iron Age (Straker & Crabtree 1995). Trees were felled for use as fuel, and as timber for building structures and tools; however, clearance for agriculture was the primary driver of deforestation (Binding 1995). Agriculture would have initially occurred at very low density in small clearings within the forest, before gradually expanding to cover wider areas. Loss of tree cover will have led to dramatic changes in soil

forming conditions, and analysis of soil under the peat layer indicates that fertile brown earth soils were far more widespread previously (Maltby 1995). The post-deforestation change to acidic, nutrient poor soils would have inhibited forest regeneration, with grazing by both wild and domesticated herbivores also acting to prevent regrowth of trees. After tree cover was lost, acidic grassland, heather moorland and blanket mire increased in prevalence. Mires developed where soils were waterlogged, while the relative proportions of grassland and heather have varied over time in relation to human land use (Straker & Crabtree 1995).

From Saxon times onwards, a large area of the moor has been used for grazing (Fyfe *et al.* 2003), which has played a major role in shaping past and present patterns of vegetation cover. Moorland on Exmoor can be divided in to three main sections: the northern and southern heather moors, and the central grass moors (Miller *et al.* 1984). It has been suggested that the reason the central moors are dominated by acid grassland is due to past high stocking levels preventing growth of heather due to its poor tolerance of grazing (Maltby 1995). Around the 14th century wool production was the major economy on Exmoor (Binding 1995), resulting in the maintenance of high stocking densities and an estimated 30,000 sheep grazing the moor by the 18th century (Maltby 1995).

Perhaps the most significant efforts to improve the moorland for agriculture started in 1818, with purchase of the former Royal Forest by John Knight. The reclamation process typically involved paring back the top surface of turf, burning the top layer, spreading the ashes, the addition of lime/slag, and then reseeding (Maltby 1995). Waterlogged soils were drained with the digging of a network of drainage ditches. Reclamation efforts continued up until the late 1900s, when addition of fertiliser began to be used as a further method of improvement (Maltby 1995). Reclamation of moorland has been a key driver behind the current heterogeneous pattern of vegetation communities on Exmoor (Miller *et al.* 1984). Where reclamation has been most successful, pastures resembling those of intensive lowland systems are present. More common are semi-improved, minerotrophic grasslands where ploughing and liming have been carried out in the past. Disturbance of the ground has led to dense stands of bracken (*Pteridium aquilinum*) in some areas, and a dominance of soft rush (*Juncus effusus*) on wetter soils. Abundance of purple moor grass (*Molinia*

caerulea) is likely to have varied historically (Chambers *et al.* 1999), but at present it dominates extensive areas of drained blanket bog.

2.1.3 Agriculture on Exmoor

The period between 1947 and 1977 saw a dramatic increase in stocking density, associated with the previously mentioned agricultural improvement efforts (Miller *et al.* 1984). Subsidy payments for farming and land reclamation also started in the 1940s, and have continued in various forms to the present. Sheep and beef cattle are commonly stocked on Exmoor, with sheep being more common. Farms are upland in nature, but differ from hill farms from more northern parts of the UK in having a lower proportion of rough grazing, and in the stocking of cattle (Dwyer *et al.* 2015). Livestock, particularly cattle, are typically only grazed on the rough pastures of the moor for the summer before being moved to winter feeding areas. Historically it has been mainly hardy breeds that have been stocked, including the Exmoor Horn, Devon Closewool and Scottish Blackface sheep, and Devon and Galloway Cattle (Wilson 1977), but improvements in agricultural practices have allowed more productive breeds to be used in some areas in recent times (Miller *et al.* 1984).

Exmoor is recognised as a 'Less Favoured Area' for farming, and therefore farmers are provided with subsidies to assist their operations; at present, farms are heavily reliant on these subsidies (Dwyer *et al.* 2015). The Higher-level Environmental Stewardship scheme, which has replaced the Environmentally-Sensitive Area scheme, allows farmers to gain subsidies through various management options aimed at improving their land for conservation, and the scheme has been taken up widely on Exmoor (Dwyer *et al.* 2015).

2.1.4 Exmoor peatlands

The majority of peat formation on Exmoor is likely to have occurred in the period following deforestation, from approximately 1600 years B.P. onwards (Merryfield & Moore 1974). Compared with many other upland areas, peatlands on Exmoor are limited in extent and relatively shallow, likely due to a combination of climate, bedrock and human activity (Straker & Crabtree 1995).

The estimated area of peat deposits on the moor is 65.28 km^2, but when peat of less than 30 cm depth is subtracted the area is reduced to 12.44 km^2 (Smith 2009). Peat deposits exist on the plateaus in ombrotrophic mires, mostly over 400 metres a.s.l., and also in the waterlogged valley bottoms. It has been suggested that blanket bog on Exmoor may be at the limit of its bioclimatic envelope, with the potential for climate change to inhibit peat formation in the near future (Gallego-Sala *et al.* 2010).

The peatlands of Exmoor have been severely degraded by drainage, with a loss of mire vegetation and an associated loss of peat forming conditions. The aim of drainage was to improve land for grazing or recreation, but it is unclear how successful this has been in terms of agricultural productivity. Drainage began in the early 19th century and continued until the late 1900s, with peat cutting for domestic use also playing a minor role in the degradation of blanket bog (Luscombe *et al.* 2016).

As elsewhere, the peatlands on Exmoor have the potential to perform valuable ecosystem services. Notably, many of Exmoor's peatlands lie within the catchment of the River Exe, which directly supplies water to over 220,000 people in the South West region (Reid 2010). As a result, the peatlands of Exmoor have a direct effect on water quality and management in the region (Grand-Clement *et al.* 2014; Luscombe *et al.* 2016). Intact peatlands can improve water quality by reducing the quantity of dissolved organic carbon into streams and rivers, thereby reducing discolouration and reducing the amount of processing required by water companies (Ritson *et al.* 2016). Intact peatlands also show reduced runoff when compared with degraded peatlands (Bragg 2002) which could potentially reduce the risk of flooding downstream, a recurrent problem in the Exe catchment. Carbon storage in peatlands means that they also provide wider value in mitigating the impacts of climate change, with Exmoor's peatlands estimated to hold the equivalent of 3.7 million tonnes of carbon dioxide (Smith 2009; Grand-Clement *et al.* 2013).

It is for these reasons that the Exmoor Mires Project has aimed to restore 2000ha of moorland to peat-forming blanket bog. The targeted areas vary in the extent of degradation, and therefore different techniques may be required for successful restoration. However, the process typically involves the blocking of

drainage ditches with peat blocks, hay bales, or wooden barriers depending on the extent of erosion (Grand-Clement *et al.* 2015).

2.2 Study sites

2.2.1 Site descriptions

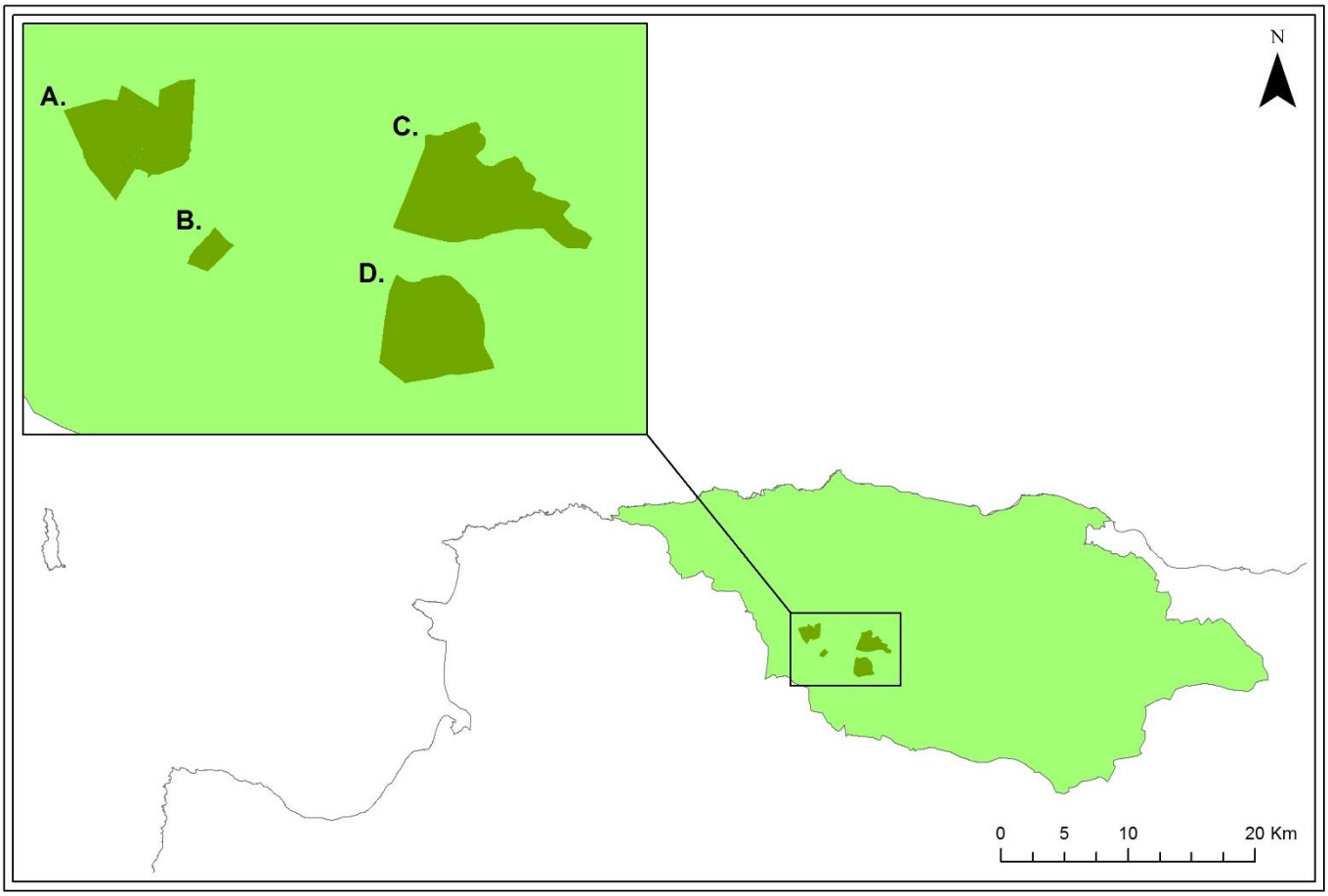


Figure 4: Map to show the locations of the study sites within Exmoor National Park. Sites are (A) Squallacombe and Aclands, (B) Hangley Cleave, (C) Spooners and (D) Long Holcombe.

Four sites, comprising five separate restoration areas, were used for this study. Aclands and Squallacombe occur within the same site boundary, but were restored at different points. The other sites, Hangley Cleave, Long Holcombe, and Spooners, are separate. All sites are located in the South West of Exmoor National park (Figure 4) within the central grass moor region.

Squallacombe and Aclands

This site is located at grid reference SS 731 384. The total area of the site is approximately 182 ha, with altitude ranging from 350 m a.s.l. in the valley bottoms to

450 m on the plateaus. There are two Exmoor Mires Project restoration areas within the site's boundaries: Squallacombe and Aclands.

At Squallacombe, restoration work was completed in 2007. The restoration area has only a small number of ditches across its centre (Figure 5), and since being blocked these have formed lines of bog pools. Squallacombe is an ombrotrophic mire, containing high-quality blanket bog vegetation. Hummock-hollow features are well developed, supporting characteristic species such as *Drosera rotundifolia* and *Empetrum nigrum* which are not found elsewhere on site. There is extensive cover of *Sphagnum* spp. and *Eriophorum angustifolium* is abundant, while *Molinia* occurs at relatively low density.

Restoration was completed at Aclands in 2014. The area consists of a catchment draining in to a gully which meets the River Barle just off site. Drainage was far more extensive here than at Squallacombe, with a dense network of ditches covering the higher areas. The restoration area surrounding the drainage ditches is dominated by tussocky *Molinia* grassland (Figure 5). Small patches of blanket bog remain, with paleoecological analysis indicating that these were previously more widespread (Fyfe *et al.* 2014).

A variety of habitats exist outside of the two restoration areas, with patches of rough and minerotrophic grassland, valley mire and flushes, dense rush pastures and bracken-covered slopes.

Hangley Cleave

This site is located at grid reference SS 742 367. Surveys here were focused on the western section of the site, covering approximately 19 ha, where peatland restoration work has been concentrated (Figure 6). The altitude of the site ranges from 410-470 m a.s.l.

Restoration work at this site was completed in 2008. A relatively small number of drainage ditches are present, and these are concentrated in the raised southern section. A small area of good quality blanket bog exists, with some poorly defined hummock-hollow features. . A large part of the site is covered by wet *Molinia* grassland, with a high frequency of *Eriophorum vaginatum* and *Juncus*. In contrast with other sites, dense, tussocky *Molinia* grassland is relatively scarce. Some patches of open minerotrophic grassland exist, and there are extensive areas of mixed *Juncus* and grassland including some sheltered by beech hedges. Valley mire communities are present in the northern part of the site, but bracken-dominated habitats are absent.

Long Holcombe

This site is located at grid reference SS 772 357. The total area of the site is approximately 179ha, with altitude ranging from 340-430a.s.l.

Restoration was completed in 2009, and drainage features are concentrated on the plateaus of the site (Figure 6). Although some areas of mire and recovering bog exist the site is relatively dry, with large areas of *Molinia*-dominated grassland. Rush pastures are extensive, and valley mire is present along the northern boundary and a central drainage gully. There are a number of patches of dry minerotrophic grassland and bracken is present on some slopes, although growth is often less dense than on other sites.

Spooners

This site is located at grid reference SS 776 374. Although the site is large, covering an area of approximately 247 ha, survey work was restricted to the western portion of the site where drainage features are concentrated (Figure 6). The altitude of the site ranges from 310-440m a.s.l.

Spooners was restored in 2013. The main west-east gully on site drains in to the River Barle. There are areas of recovering bog at the head of the gully and on the surrounding plateaus, but these are typically dominated by *Molinia.* Patches of quality blanket bog are small and isolated, but may contain scarce mire species such as *Vaccinium oxycoccos.* Tussocky *Molinia* grassland covers

a large part of the site. Other habitats include dry, minerotrophic grassland, bracken-dominated slopes, valley mire and rush pasture, included some sheltered within a small enclosure lined by beech trees.

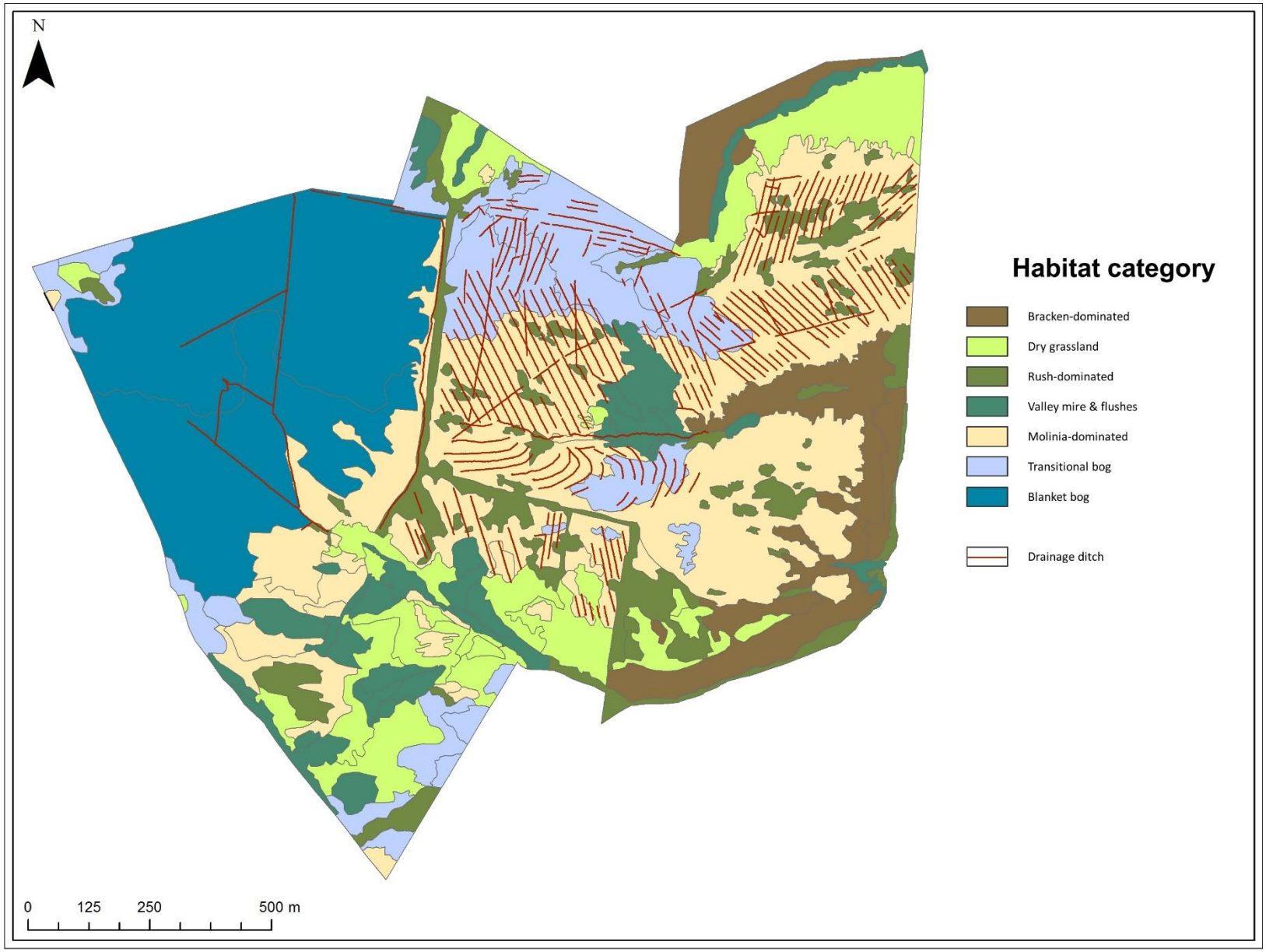
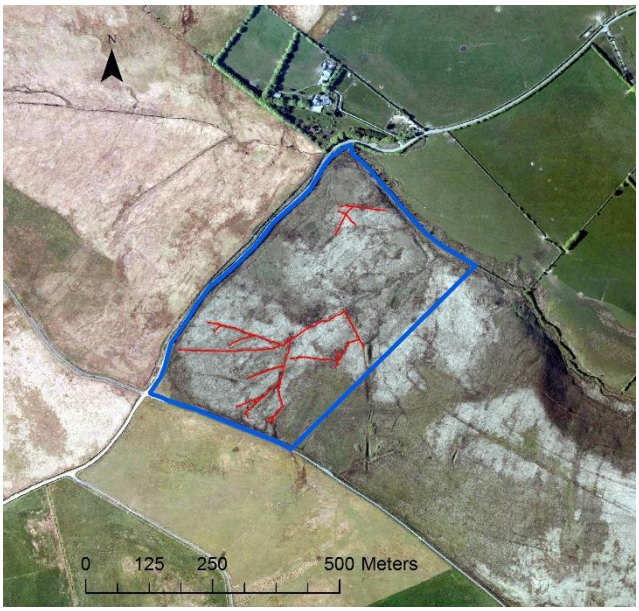


Figure 5: Distribution of different habitat categories and drainage ditches at Squallacombe and Aclands.

A.



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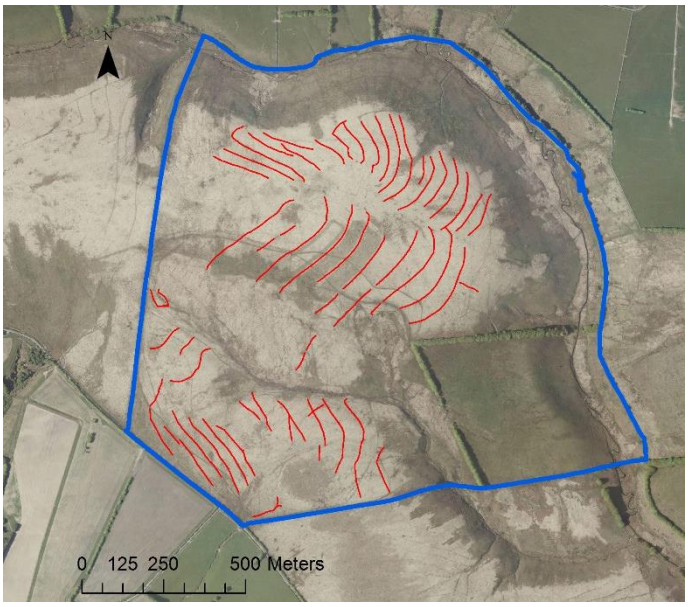

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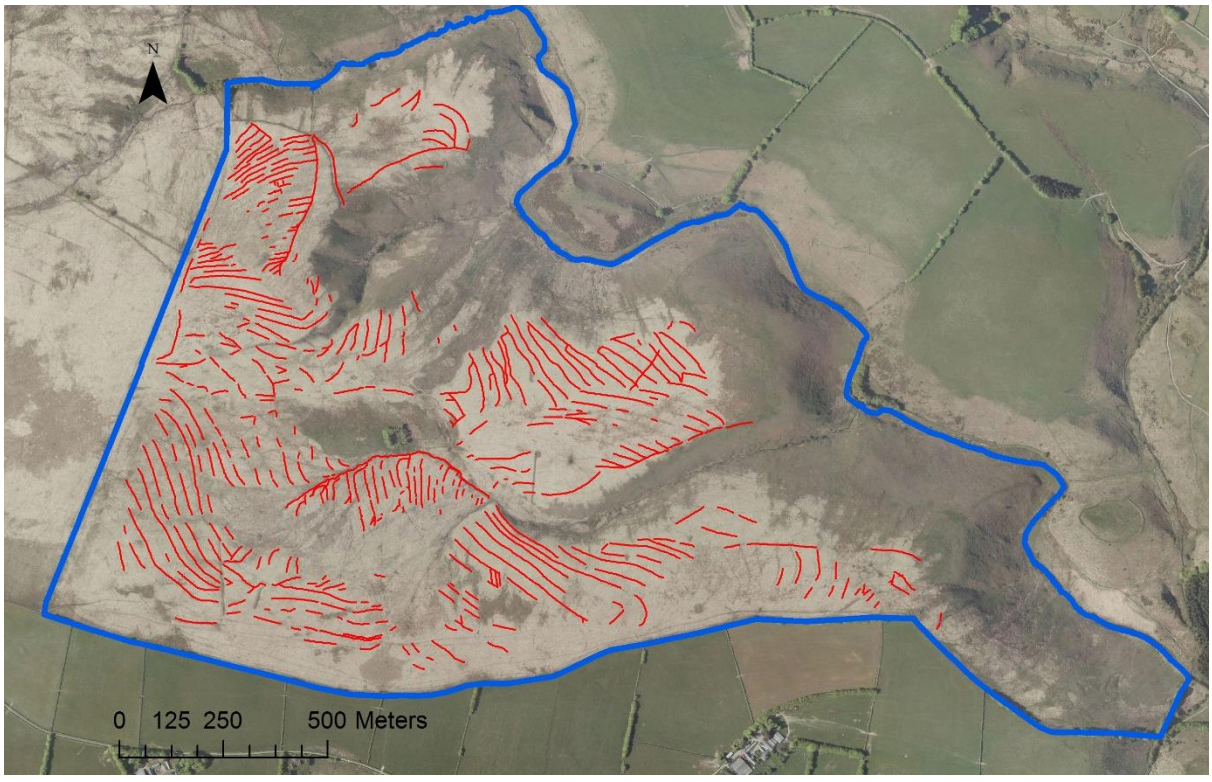


Figure 6: Aerial photographs of (A) Hangley Cleave, (B) Long Holcombe and (C) Spooners. Blue lines show site boundaries, and red lines show the locations of drainage ditches.

2.2.2 Habitat mapping

Habitat maps were based on some previous work carried out as part of the Exmoor Mires Project, but I extensively updated this based on high definition satellite photographs and field surveys. The previous survey work provided a coarse outline of the distribution of various habitats on site, but some habitat boundaries have changed since the work was undertaken. As a result, I updated every habitat boundary in order to provide an accurate reflection of the distribution of different vegetation communities, and numerous new patches of vegetation were mapped. I used high definition aerial photographs as an effective means of delineating habitats, with separate habitat patches being identified by differences in colour. ARCMap 10.3 software was used to map these habitat boundaries by tracing the outline of discrete habitat patches, thereby creating a detailed map of the sites' habitats. Habitat survey work was carried out at Squallacombe and Aclands as these sites were the focus of vegetation monitoring and grazing studies. I validated habitat patches identified in the aerial photographs with field surveys, with each separate patch being visited and assigned to a habitat type. Field surveys and mapping in ARCMap were completed over a period of three weeks in the early spring of 2016. I spent four days on site to carry out the field surveys, while the mapping in ARCMap took approximately 24 hours in total, spread over the three week period. Identification of different habitats was based on differences in species composition and physiognomy of plant communities, with each different habitat being placed in a category. On visiting the next patch, the community would either be assigned to a previous category if it corresponded to a previously surveyed habitat, or placed in a new category if it was a new vegetation type. This was continued until all habitat patches on the site had been visited, giving a total of 23 different vegetation community types. Patches consisting of fine-scale mixtures of vegetation communities were poorly defined in aerial photographs. However, where a patch was found to consist of discrete areas of two or more vegetation communities this was noted as a mixture rather than being designated as a new vegetation type. Each of the 23 vegetation communities were assigned to a broad-scale habitat category to allow comparison between habitats at a larger scale. Assignment to category was based on dominant plant species, vegetation structure and characteristics of the

habitat such as wetness. The broad scale habitat categories used in this study, along with the numbered vegetation communities that they contain, are described here.

Bracken-dominated

These are the only communities containing bracken; however, due to the dominant nature of bracken it occurs at high densities where present, typically accounting for a large proportion of the total vegetation cover and resulting in a low diversity of other plant species. These communities occur on well-drained, fertile soils which have been subject to improvement efforts in the past. Bracken responds well to disturbance, so areas where it dominates may have been burned or ploughed previously. Descriptions of the two bracken-dominated habitats are given in Table 1, and their distribution is shown in Figure 7.

Dry grassland

Habitats in this category contain a mix of vegetation communities, reflecting different levels of past agricultural improvement. Patches are more open and uniform in terms of physiognomy when compared with other habitat categories. Soils are typically well drained, and aside from occasional tussocks of *Molinia* or stands of *Juncus,* the vegetation is low-growing. Where agricultural improvement efforts have been less sustained there are patches of rough grazing, dominated by moorland species such as *Nardus stricta*. However, in places where improvement has been more intensive there is a greater diversity of minerotrophic grass species such as *Agrostis* spp. and *Festuca* sp. These habitats have a fairly high diversity of species, and often contain dwarf-shrubs and herbs along with a dense bryophyte ground layer. Habitats within this category are described in Table 2, and their distribution is shown in Figure 8.

Rush-dominated

All habitats within this category share a high *Juncus effusus* cover and occur on relatively dry ground. Associated plant assemblages can be fairly diverse, depending on the density of rush, and typically consist of species which favour drier conditions. Rush-dominated habitats occur in improved patches, and particularly those which have been disturbed by, for example ploughing. The ability to dominate disturbed ground means that stands of *Juncus* often line

drainage ditches. Habitats within this category are described in Table 3, and their distribution is shown in Figure 9.

Valley mire and flushes

These vary in species composition, but are characterised by consisting of tall, rank vegetation on extremely wet ground fed by flushes and streams. The dominant species is either *Molinia caerulea* or *Juncus effusus*, and often species diversity is low due to the extensive cover of these larger species. Depending on the community there may be characteristic species such *as Juncus articulatus* and *Cirsium palustre*, neither of which are found in the ombrotrophic mires. The extremely wet nature of these habitats means that they have received little human disturbance in terms of reclamation effort. Community types falling under this category are described in Table 4, and their distribution is shown in Figure 10.

Molinia-dominated

These habitats differ slightly in character, but share *Molinia caerulea* as their dominant species. The large size of *Molinia* along with its tussock forming nature mean that it can outcompete other species, with a low diversity of associated plants as a result. *Molinia* occurs as a component of dry and wet habitats, but the dense monocultures are typically restricted to wetter areas. Draining of blanket bog is thought to have produced the extensive tracts of *Molinia* currently present on the moor, with drier conditions resulting in loss of mire species while favouring *Molinia*. Communities within this category are described in Table 5, and their distribution is shown in Figure 11.

Transitional Bog

Molinia is often dominant in these habitats, but they show characteristics of blanket bog and may be in the process of conversion. Presence of *Sphagnum* spp. is a key feature, while other mire species such as *Eriophorum* sp. are also present at varying densities. Some patches may have a predominantly mire vegetation community, but they lack the full diversity of species present in pristine mire. These habitats occur on degraded peatland, with the direction of future vegetational succession likely depending on environmental conditions.

The three habitats within this category are described in Table 6, and their distribution is shown in Figure 12.

Blanket Bog

These communities are indicative of high-quality blanket bog. Hummock and hollow features are well developed, and *Sphagnum* cover is high. Mire species diversity is also high, with good cover of *Eriophorum angustifolium* and the presence of indicator species such as *Drosera rotundifolia*. These habitats are found on wetter areas of the plateaus. The aim of ditch-blocking operations is to regenerate areas of blanket bog through rewetting. The two communities within this category are described in Table 7, and their distribution is shown in Figure 13.

2.3 Conclusion

Exmoor supports a variety of characteristic upland habitat types, the distribution of which are dictated by past and present land use. The prevalence of different habitats has varied over time and is likely to continue to change, with management practices determining the direction of future change in vegetation communities. Agriculture remains as the dominant land use on Exmoor, and due to the extensive, semi-natural character of pastures, vegetation change has potential to affect the productivity of grazing. On Exmoor's pastures there are a number of drivers with the potential to alter vegetation communities. These may include processes which are predominantly natural, such as interannual climate variability and ecological succession, and those which are anthropogenic in nature, such as reclamation for agriculture or restoration for conservation purposes. With the increase in peatland rewetting, a reduction in the prevalence of *Molinia*-dominated pasture and an increase in bog is one habitat change which is expected to occur. However, as peatlands typically exist within grazing sites, and one of the reasons for drainage was agricultural improvement, these changes could have an impact on the grazing value of pastures. Vegetation change is a relatively obvious indication of ecosystem change, and it could potentially affect agriculture in a number of ways. Change in vegetation community structure might affect the distribution and abundance of high-quality forage species, or the prevalence of favourable grazing habitats. Furthermore, the abundance and distribution of parasites and arthropod-vectors exhibiting

fine-scale microhabitat preferences could be affected by vegetation change, with an associated change in livestock disease risk. The aim of this study was to assess the agricultural productivity of Exmoor peatland restoration sites based on differences between habitats in sward quality, livestock grazing preferences and parasite prevalence.

Table 1: Description of bracken-dominated vegetation communities found within the study sites on Exmoor National Park; see also Figure 7.

Number	Description	Identifying Features	Occurrence
1	Dense bracken	High density of tall bracken with a species-poor understory of grass species such as *Holcus lanatus*	Restricted to well drained, steep slopes
2	Bracken and dry grass	Bracken at high density, but individual plants typically shorter than in 1. Open areas between bracken, with a fairly diverse mix of grass species.	Mainly restricted to drier slopes, but also on flatter ground near valley bottoms

Table 2: Description of dry grassland vegetation communities found within the study sites on Exmoor National Park; see also Figure 8.

Number	Description	Identifying Features	Occurrence
3	Rough *Nardus* grassland	*Nardus stricta* is dominant. Species diversity is relatively high, but no other species attain high densities due to the dominance of Nardus.	Present in damp improved areas on slopes and plateaus
4	Rough *Deschampsia* grassland	Has similar characteristics to 3, but *Deschampsia cespitosa* replaces *Nardus* as the dominant species.	Present in damp improved areas on slopes and plateaus

5	Rough grassland	Essentially a mix of the two preceding habitats, with roughly equal cover of *Nardus* and *D. cespitosa*.	Present in damp improved areas on slopes and plateaus
6	Minerotrophic grassland	Predominantly minerotrophic grasses such as *Festuca*, *Agrostis* and *Anthoxanthum odoratum* growing through a dense mat of bryophytes. Moorland grasses are present but at low density.	Occurs in well drained improved areas, often on slopes.
7	Acidic grassland	Similar to 6, but contains a higher proportion of moorland species such as *Danthonia decumbens* and *Carex binervis*. Dwarf-shrubs such as *Vaccinium myrtillus* occur at very low density.	Occurs in well drained improved areas on slopes.
8	Grassland and heath	Similar to 7, but contains higher cover of dwarf-shrubs, including *Calluna*, and a higher proportion of moorland species such as *Nardus*. Bryophyte cover is high.	Occurs in well drained improved areas on slopes.

Table 3: Description of rush-dominated vegetation communities found within the study sites on Exmoor National Park; see also Figure 9.

Number	Description	Identifying Features	Occurrence
9	Dense damp Rush	Very high percentage cover of tall *Juncus*. Grows over damp, rank grass where *Holcus lanatus* makes up the majority of understorey cover.	Found in damp improved areas
10	Dense dry Rush	Very high density of tall *Juncus*, with a fairly diverse understorey of minerotrophic grassland species, bryophytes and herbs.	Present in better drained improved areas and along drainage ditches
11	Rush and grassland	*Juncus* is dominant, but sparser and shorter than in 9 and 10, growing among obvious patches of predominantly minerotrophic grass species.	Found on well drained improved slopes and in patches among *Molinia*

Table 4: Description of valley mire and flush vegetation communities found within the study sites on Exmoor National Park; see also Figure 10.

Number	Description	Identifying Features	Occurrence
12	Rush-dominated flush	Predominantly dense, tall *Juncus effusus*, with *Molinia* occurring at very low density. *Sphagnum* spp. and *Polytrichum commune* are frequent.	Occurs in isolated patches where seepages occur on slopes, and in valley bottoms.
13	*Molinia*-dominated flush	Very wet ground with large tussocks of rank *Molinia* dominating. Low diversity of other species, but *Juncus articulatus* may be present.	Can cover large areas where flushes occur on hillsides, also in some valley bottoms.
14	Rush and *Molinia* flush	*Juncus effusus* and *Molinia* occur at roughly equal density. Contains a number of species such as *Cirsium palustre*, *Juncus articulatus*, and *Epilobium palustre*, which are scarce or absent in other habitats.	Present in similar areas to, and often alongside 13.
15	Valley mire	Very wet ground with *Juncus effusus* dominant, and *Holcus lanatus* reaching higher densities than *Molinia*. *Carex rostrata* reaches moderate densities in the wettest areas.	Occurs in isolated patches in valley bottoms.

Table 5: Description of *Molinia*-dominated vegetation communities found within the study sites on Exmoor National Park; see also Figure 11.

Number	Description	Identifying Features	Occurrence
16	Dense *Molinia*	Extremely dense cover of tussocky, rank *Molinia* on fairly damp ground. A small number of other species are present, but all at very low density.	Covers large areas of the plateaus, particularly in drained areas.
17	*Molinia* and Rush	*Molinia* is dominant, with individual plants or small patches of *Juncus effusus* occurring intermittently. Diversity is higher than 16, with a number of grass species growing among the *Juncus*.	May cover large areas, typically on slightly drier ground than 16.
18	Dry *Molinia*	*Molinia* is dominant, but tussocks are interspersed with small patches on minerotrophic grass species and bryophytes.	Occurs in dry, well-drained areas, often on the periphery of areas of 16.

Table 6: Description of transitional bog vegetation communities found within the study sites on Exmoor National Park; see also Figure 12.

Number	Description	Identifying Features	Occurrence
19	Wet *Molinia*	A very high density of *Molinia*, but with sporadic occurrence of mire indicators such as *Sphagnum* spp. and *Eriophorum vaginatum*.	May cover large areas on damp ground on plateaus.
20	Wet *Molinia* and Mire	*Molinia* is dominant, but diversity and abundance of mire species is higher than in 1. Species favouring drier conditions are also frequent.	May cover large areas of wet ground on plateaus.
21	Recovering Mire	Good quality bog with low density of *Molinia*, high cover of *Sphagnum* spp. and mire plant species such as *Eriophorum angustifolium* and *Narthecium ossifragum*.	May cover large areas of wet ground on plateaus.

Table 7: Description of blanket bog vegetation communities found within the study sites on Exmoor National Park; see also Figure 13.

Number	Description	Identifying Features	Occurrence
22	Mire hollow	The very wet ground between hummocks is dominated by *Sphagnum* spp. and *Eriophorum* sp. Characteristic mire species such as *Narthecium ossifragum* and *Drosera rotundifolia* are frequent.	Occurs on wet, rain-fed, flat ground.
23	Mire hummock	The drier hummocks are still dominated by *Sphagnum*, but have a higher density of dwarf-shrubs such as *Calluna vulgaris*, *Vaccinium myrtillus* and the characteristic *Empetrum nigrum*.	Occurs with 22 to form a mosaic of hummock-hollow communities.

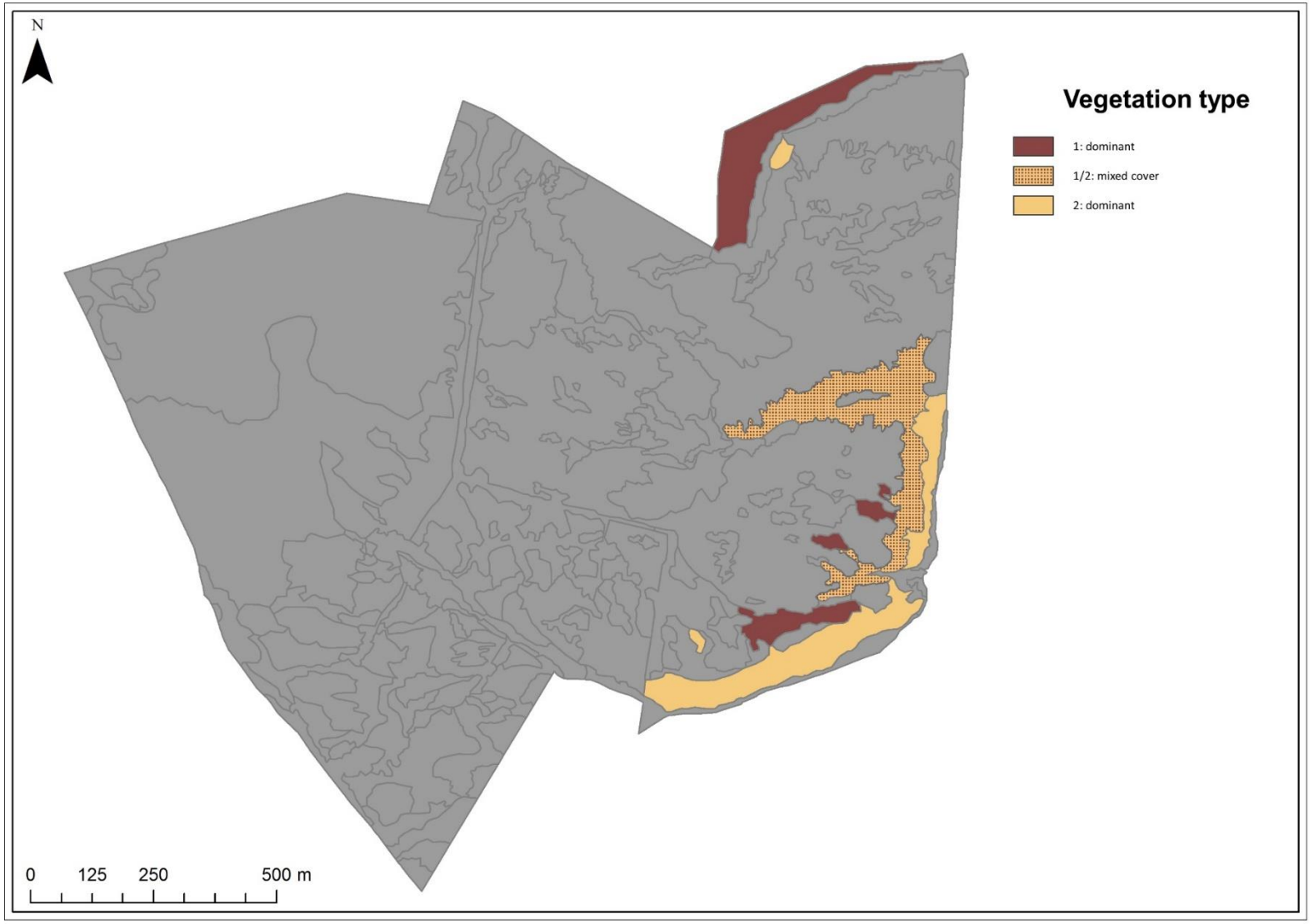


Figure 7: Distribution of bracken-dominated habitats on Squallacombe and Aclands. Community descriptions are given in Table 1.

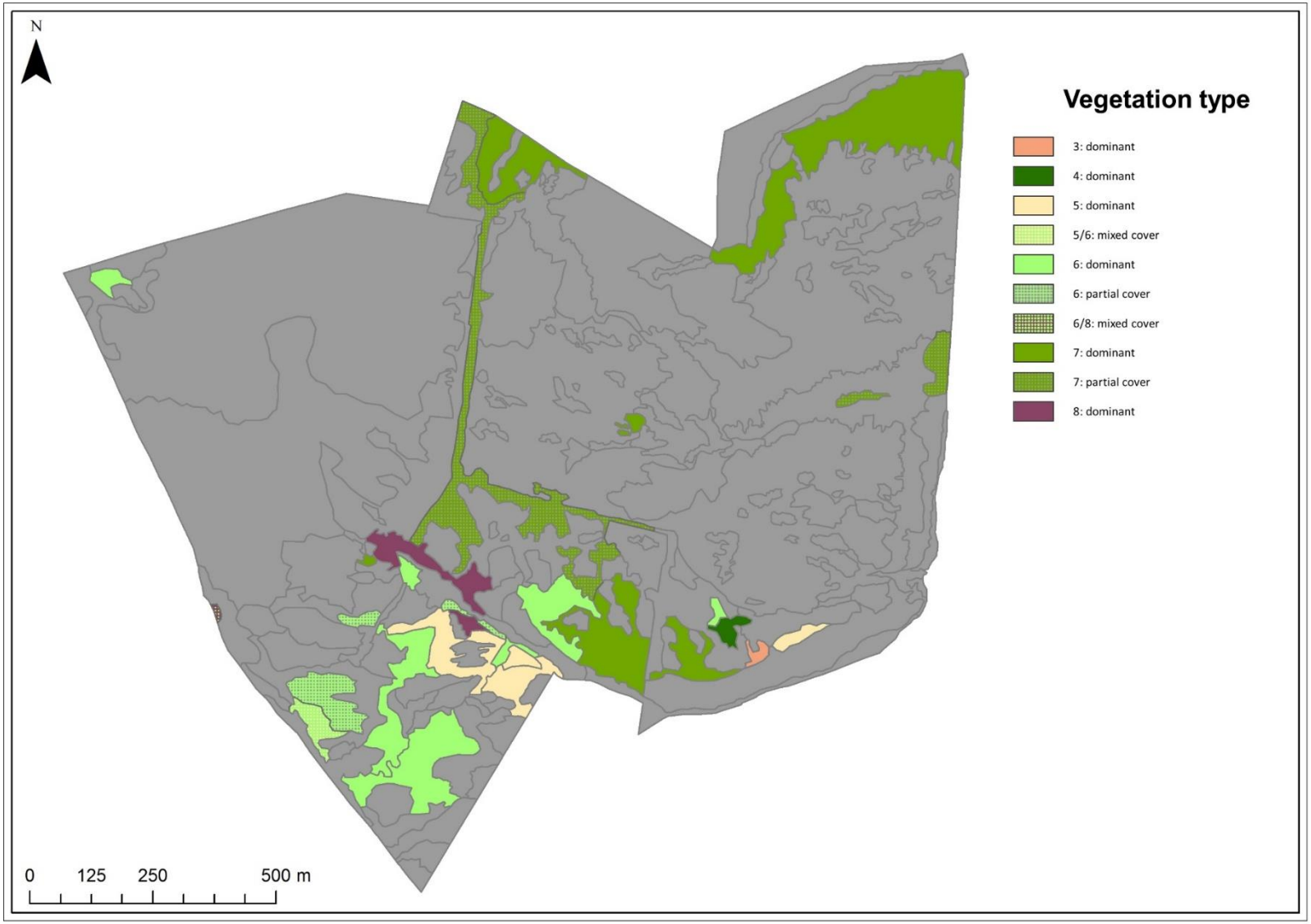


Figure 8: Distribution of dry grassland habitats on Squallacombe and Aclands. Community descriptions are given in Table 2.

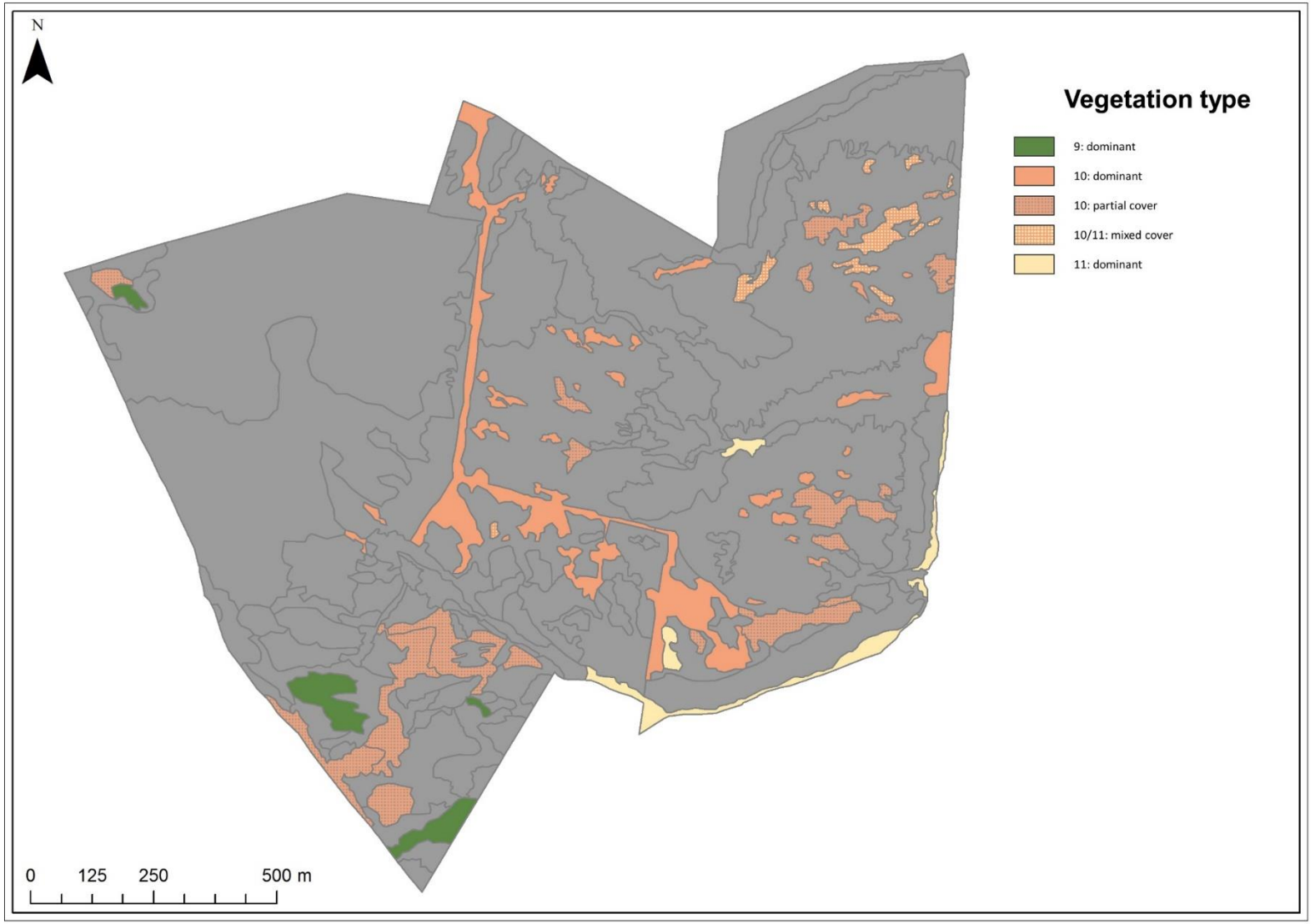


Figure 9: Distribution of rush-dominated habitats on Squallacombe and Aclands. Community descriptions are given in Table 3.

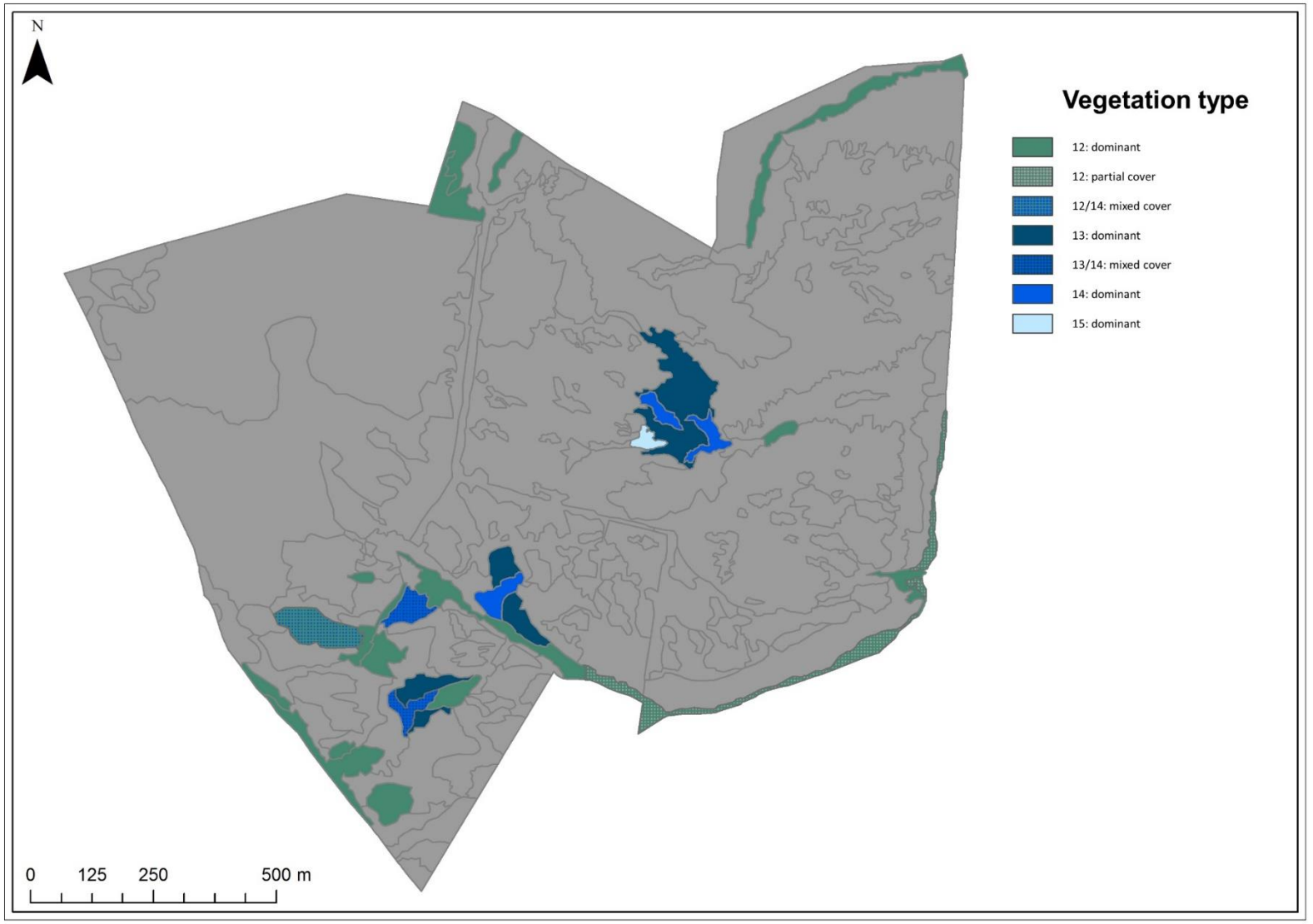


Figure 10: Distribution of valley mire and flush habitats on Squallacombe and Aclands. Community descriptions are given in Table 4.

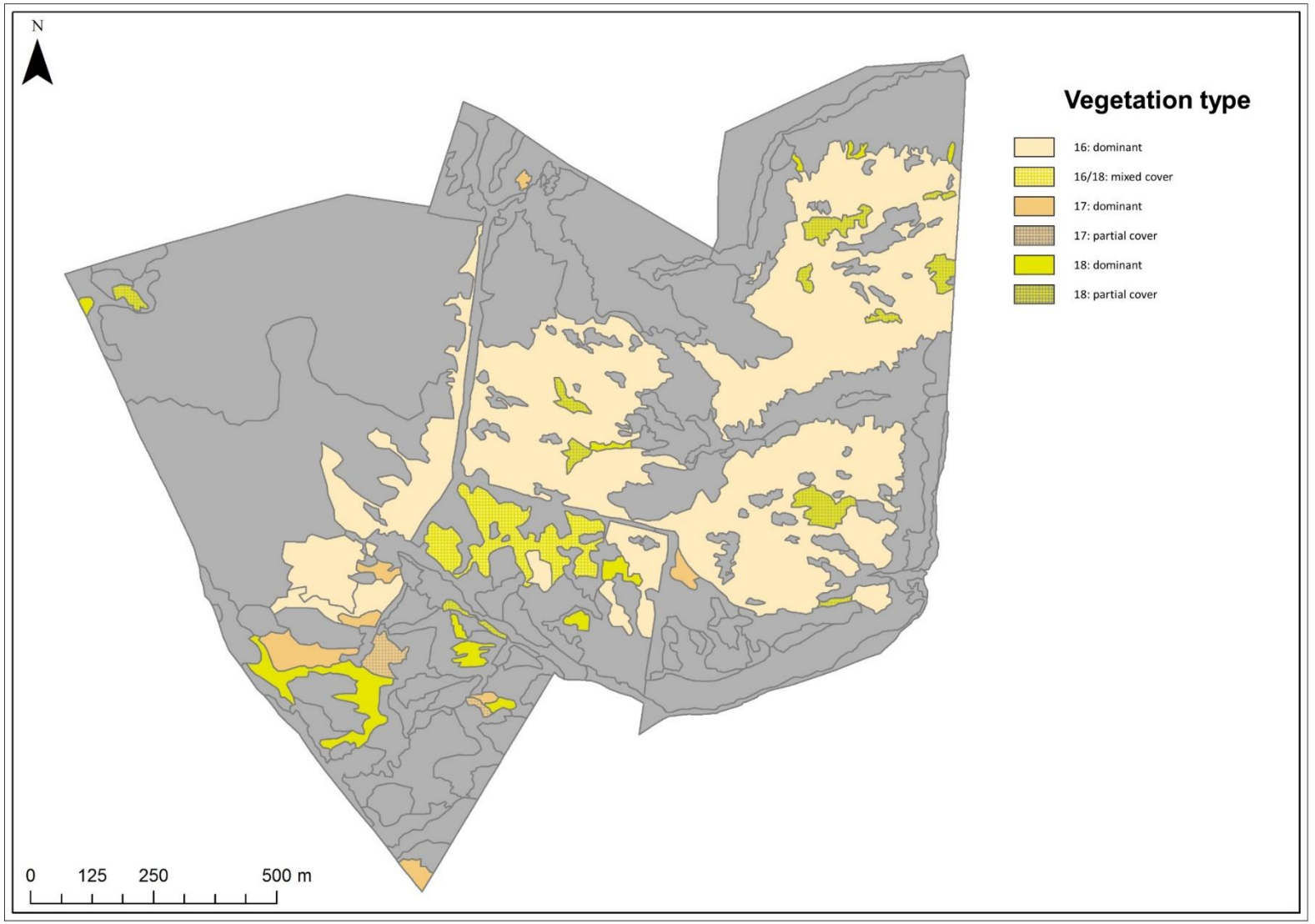


Figure 11: Distribution of *Molinia*-dominated habitats on Squallacombe and Aclands. Community descriptions are given in Table 5.

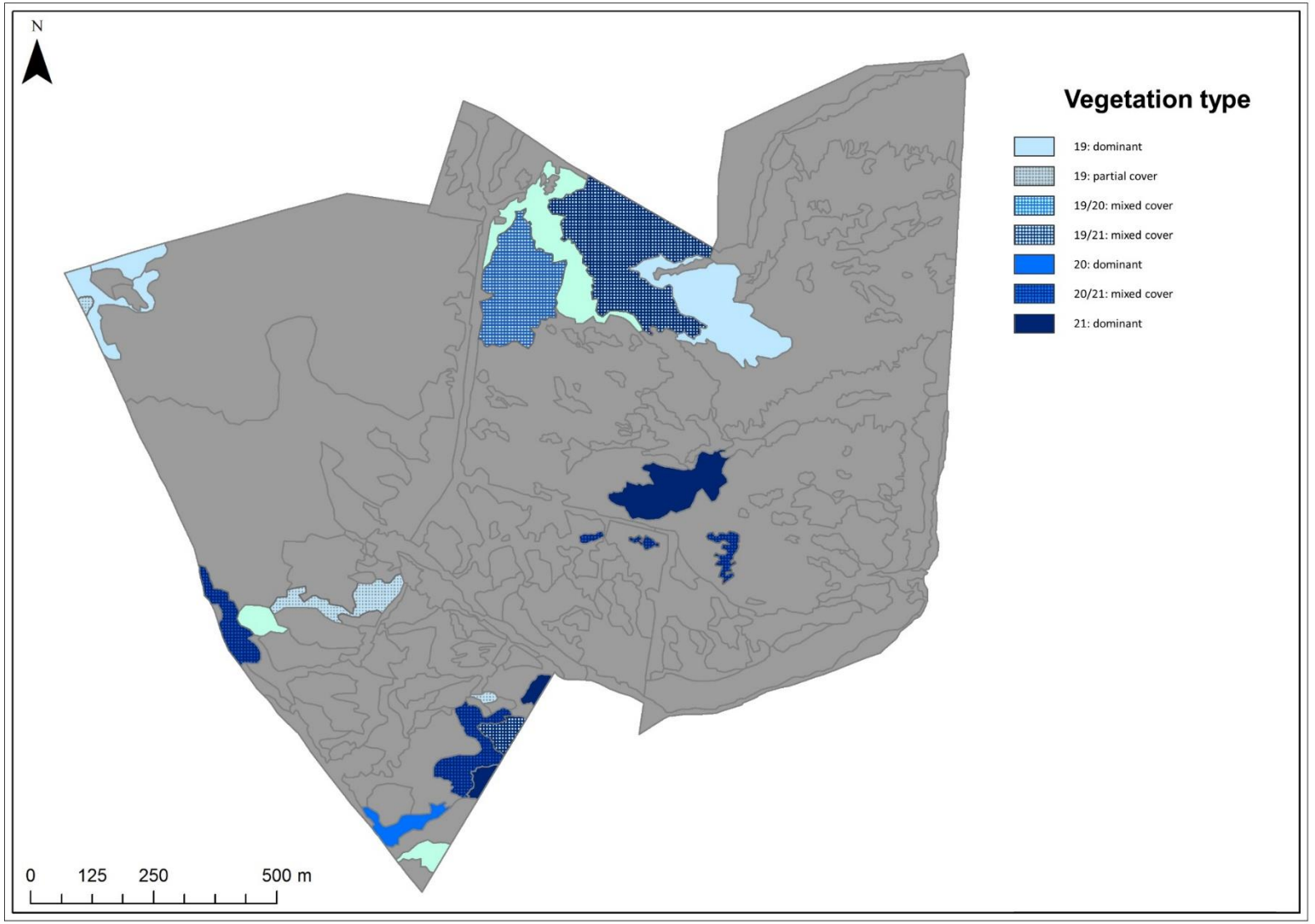


Figure 12: Distribution of transitional bog habitats on Squallacombe and Aclands. Community descriptions are given in Table 6.

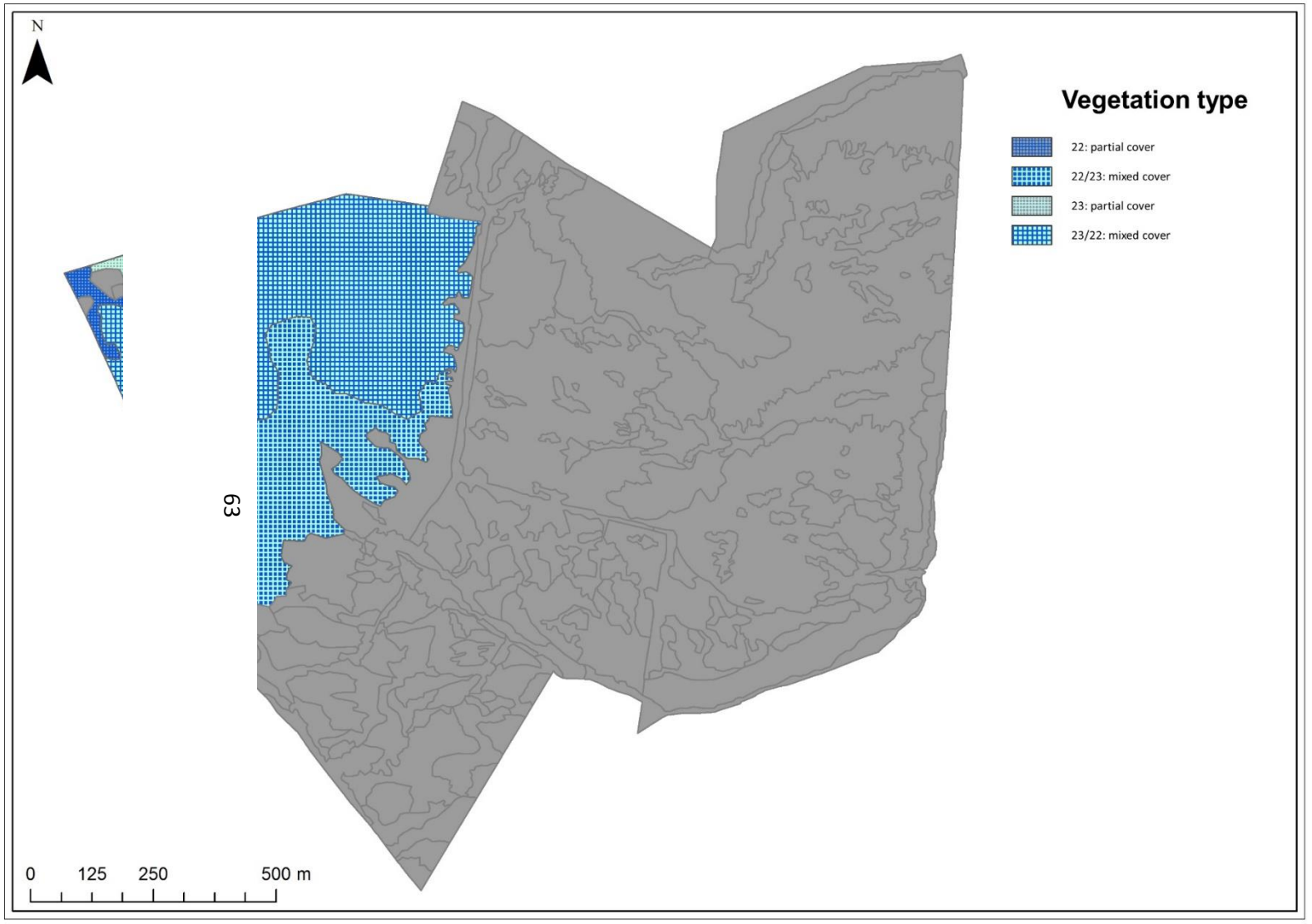


Figure 13: Distribution of blanket bog habitats on Squallacombe and A
Community descriptions are given in Table 7.

Chapter 3: Sward quality in upland pastures

3.1 Background

3.1.1 The effects of ecosystem change on vegetation

Vegetation communities have been altered by human activity, and there are likely to be few which have not been affected to some extent (Vitousek 1997a). The response of communities to environmental change is variable, but changes in abiotic and biotic processes can have a dramatic impact on an ecosystem's vegetation structure (Scheffer *et al.* 2001; Scheffer & Carpenter 2009). Among abiotic processes, recent climate change driven by rising levels of CO_2 has been demonstrated to drive changes in vegetation communities (Walther *et al.* 2002). Cold climate assemblages may be particularly vulnerable to increases in temperature, with warmer conditions shown to alter the species composition of montane (Harte & Shaw 1995; Gottfried *et al.* 2012) and Arctic tundra communities (Chapin III *et al.* 1995; Sturm *et al.* 2001; Elmendorf *et al.* 2012), driving shifts in their altitudinal and latitudinal distribution respectively (Parmesan 2006). In addition, changes to the carbon cycle have the potential to alter plant species composition due to interspecific differences in their growth rates under higher atmospheric levels of CO_2 (Taub 2010).

Water availability is another important factor, with alterations of regional hydrology having a profound impact on the structure of vegetation communities (Gordon *et al.* 2008). Any vegetation type may be affected by changes in hydrology, but the impact can be particularly severe in those assemblages occurring within or adjacent to water bodies, such as wetland, riparian, and freshwater communities (Stromberg *et al.* 1996; Bunn & Arthington 2002; Tockner & Stanford 2002; Graf 2006).

Changes in nutrient loading can also lead to dramatic changes in vegetation structure, with input of nitrogen and sulphur, among others, affecting species diversity and abundance (Vitousek 1997b; Lee 1998; Krupa 2003)). Alteration of the nitrogen cycle has increased its availability within many ecosystems, which can cause loss of freshwater plant communities through eutrophication of water bodies (Smith *et al.* 1999; Smith 2003), and loss of diversity in grassland communities adapted to nutrient poor conditions (Dupre *et al.* 2010). Both

nitrogen and sulphur deposition result in acidification of soil, with a knock on effect for vegetation communities and potential loss of species favouring more base-rich conditions (Hogg *et al.* 1995).

Among biotic processes, biological invasion is significant as a driver of change in vegetation communities (Mack *et al.* 2000; Pysek *et al.* 2012). Alien plants may dominate new environments where conditions allow them to become established (Seabloom *et al.* 2003), and once present they may alter their new environment in a way which makes it unfavourable for the growth of native competitors (D'Antonio & Vitousek 1992), resulting in a loss of plant species diversity in the ecosystem. Invasion by alien herbivores can also lead to dramatic changes in vegetation structure, with some species poorly equipped to sustain the pressure of predation (Kenis *et al.* 2009). Similarly, the arrival of an alien pathogen may result in decreased abundance or loss of affected species, with the potential for resulting change in ecosystem structure in the invaded region (Crooks 2002).

Outbreaks of native pest species may have a severe impact on vegetation structure within a community, particularly where compounded by other factors such as climate change (Bentz *et al.* 2010), but these changes are frequently short term and cyclic in nature (Bengtsson *et al.* 2000).

Vegetation structure is often simply altered by mechanical disturbance and clearance, with processes associated with human land use, such as deforestation, ploughing and grazing, resulting in immediate changes to the composition of vegetation communities (Foley *et al.* 2005; Laurance et al, 2014).

Vegetation typically makes up a significant component of ecosystem structure, and as a result can have a major effect on ecosystem function (Grime 1998), with aspects such as cover and diversity directly affecting ecosystem processes such as soil respiration and nutrient cycling (Zak *et al.* 2003; Moco *et al.* 2005). Therefore, loss of vegetation, or a shift to an alternative community, has the potential to alter ecosystem functionality. For example, environmental perturbations may lead to vegetation changes which affect the hydrology of ecosystems by modifying flow regimes and water storage (Bosch & Hewlett 1982; LeBlanc *et al.* 2008), or alter soil nutrient cycling processes (Hobbie 1992; Ehrenfeld 2003). Furthermore, as ecosystem gas fluxes are largely

defined by plant processes such as photosynthesis and evapotranspiration, a change in vegetation cover can have a direct effect on local climate patterns (Osborne *et al.* 2004; Gatis *et al.* 2015; Gatis *et al.* 2017).

As vegetation plays an important role in ecosystem functionality, changes in composition have the potential to affect the diversity and quantity of ecosystem services provided. Plant communities contribute to a number of highly valued ecosystem services (Daily *et al.* 2000; Balmford *et al.* 2002; Costanza *et al.* 2014). Vegetation can provide disturbance regulation, with intact vegetation cover regulating water flow after high rainfall (Guo *et al.* 2000), and coastal habitats such as mangroves and saltmarsh acting to reduce the impact of storm events (Borsje *et al.* 2011; Gedan *et al.* 2011). Vegetation also plays an important role in climate regulation through carbon sequestration in plants, for example in forests and intact blanket bog (Stenger *et al.* 2009; Pan *et al.* 2011). The plants of an ecosystem are also important for the supporting services that they provide, as in the previously mentioned nutrient cycling and in providing refuge and food for species groups of economic value such as pollinators (Kearns *et al.* 1998; Potts *et al.* 2010). Vegetation is also highly valued for provisional services, such as timber and food, and grazing for livestock, with pasture lands making up a significant proportion of human land use (Asner *et al.* 2004).

Human land use may also have a negative impact on global ecosystems (Vitousek *et al.* 1997a), and change in vegetation communities has the potential to further alter ecosystem processes and ecosystem service provision. For this reason, a vast number of restoration projects exist globally with the intention of regenerating vegetation cover or species diversity in order to improve biodiversity and restore ecosystem function (Aronson *et al.* 2006). The success projects varies greatly (Benayas *et al.* 2009), but there are examples of successfully increasing the provision of ecosystem services through the recovery of vegetation (Koch & Hobbs 2007; Jenkins *et al.* 2010).

3.1.2 Vegetation change in upland environments

Human activity has driven change in the vegetation communities of uplands in the UK. Shortly after the last glacial maximum, improving climatic conditions lead to regeneration of forest cover across much of the UK. It is likely that all but the highest peaks would have been covered by forest, and relatively low altitude uplands such as Exmoor and Dartmoor would have had almost blanket tree cover (Averis *et al.* 2004). The type of forest varied with geography and altitude, with pine and birch being more extensive at higher altitudes and latitudes, and broadleaved woodland dominating in lower areas (Burt *et al.* 2002).
Starting around 5000-6000 years B.P., humans began clearing the uplands of forest cover in order to obtain materials and to open the land for other uses such as agriculture (Reed *et al.* 2009). Deforestation has had a profound impact on the uplands, leading to the infertile, open landscapes of today (King 1977). Loss of tree cover combined with human land use following deforestation has led to the current pattern of vegetation seen in uplands today (Miles 1987).

Despite being widely separated, the UK's upland areas bear many similarities in the vegetation communities which they support. Certain communities are restricted by environmental variables; for example, montane communities only occur on peaks of suitable altitude, such as those in Scotland (Averis *et al.* 2004). However, other habitats are considerably more widespread, and reflect similarities in patterns of human land-use and land management across the uplands (Ball *et al.* 1981).
Two of the more frequent upland habitats are rough, acid grassland and heather moorland, with the relative proportions of these in different upland areas reflecting past and present land use (Miles 1987). Both occur in relatively well drained soils; either those which are naturally drier such as on steep slopes, or those which were previously wetter but have been reclaimed through the digging of drainage ditches. Heather moorland is prevalent where grouse shooting is the dominant land use, with a regular rotation of burning used to promote fresh heather growth and maintain high cover (Thompson *et al.* 1995). However, heather is unable to support high grazing pressure, and areas used for the production of hill sheep or cattle may see a loss of heather and a change to other vegetation communities (Anderson & Yalden 1981). Over-grazing of

heather usually results in a switch to grassland which, depending on soil characteristics and the underlying seed bank, is typically dominated by *Molinia caerulea* on wetter soils, or *Agrostis* spp., *Festuca* sp. and *Nardus stricta* on drier soils (Miles 1987).

Agricultural improvement may produce other grassland communities. In places which have seen intensive improvement efforts, including ploughing, addition of lime, addition of fertiliser and reseeding, pastures may resemble those of the more fertile, managed lowlands with cover of *Lolium perenne* and *Trifolium repens* (Maltby 1995). However, more typically the grasslands maintain at least some of their moorland character. Patches of ground which have been ploughed, burned, limed and reseeded produce communities of minerotrophic grasses such as *Agrostis* spp. and *Festuca* sp. (Miles 1987), which are less coarse than those species of rough grassland such as *Molinia*. Grazing of these patches can help to prevent succession through colonisation of more robust species, allowing these communities to persist for long periods (Hulme *et al.* 1999).

Environmental perturbations, such as burning or mechanical disturbance of the soil, may lead to the dominance of species which are able to rapidly monopolise disturbed ground. Dense patches of *Juncus* and bracken may develop due to such disturbances (Miles 1987). While smaller grasses and herbs may occur in the understorey of these plants, their robustness means that patches of these species are likely to persist without considerable intervention.

Where land reclamation has not been attempted on waterlogged soils wetland communities occur, with the character of these depending on their water source. On plateaus and gently sloping land, rain-fed ombrotrophic mire may develop. The blanket bog communities of ombrotrophic mires form peat through the slow decomposition of species such as *Sphagnum* spp., and they may sit on top of very deep deposits (Lindsay 2010). Where seepages and flushes occur, valley mire communities develop. These are typically more nutrient rich, and as a result have a different suite of plant species, with limited presence of *Sphagnum* and a higher cover of coarse grasses and *Juncus* (Averis *et al.* 2004). Blanket bog is extremely vulnerable to excessive nutrient loading, for

example though atmospheric nitrogen deposition (Hogg *et al.* 1995), and all wetland communities may be negatively affected by changes in hydrology where drainage has taken place (Miles 1987).

3.1.3 Peatland restoration and vegetation change

Drainage of peatland typically results in a change to grassland or forest communities, although the extent and severity of change vary due to differences in drainage technique and topography of sites (Ramchunder & Holden 2009). Recently there have been an increasing number of projects aiming to restore degraded peatlands to their naturally functioning state due to the ecosystem services this can provide, and measuring vegetation change is frequently used as a means of determining whether a restoration project has been successful.

Different restoration projects involve different levels of intervention, and this appears to have an effect on their levels of success. The passive form of peatland restoration is through abandonment of the damaging processes in order to allow the recovery of vegetation. In degraded peat areas of Canada, recovery of bog species depends on the previous method of harvesting used, and abandonment alone is not enough to regenerate a functioning peatland community (Lavoie & Rochefort 1995). Abandoned peat harvesting areas can regenerate good cover of bog species over time, but they often contain a higher proportion of dry indicators such as trees when compared to pristine habitats (Kollmann & Rasmussen 2012). Where key species such as *Sphagnum* recolonise they can potentially assist the regeneration of bog communities due to their manipulation of their environment, but their spread is limited by areas of lowered water table (Price & Whitehead 2004). Manipulation experiments in the same degraded peatlands indicate that rewetting through ditch blocking will enhance the recovery of blanket bog vegetation when compared to abandonment alone (Gonzalez *et al.* 2014).

Rewetting of peat through the blocking of drainage ditches is a common form of intervention in restoration schemes (Grand-Clement *et al.* 2015). Blocking of drainage ditches has been shown to increase the cover of blanket bog species, and subsequently decrease the cover of those species favouring drier

conditions (Bellamy *et al.* 2011). Some studies have not identified any major changes in vegetation communities following rewetting, perhaps due to insufficient timescales (Urbanova *et al.* 2012) or a reasonably intact mire community having already been present in the peatland's degraded state (Laine *et al.* 2011). However, as presence of bog vegetation is related to depth of the water table (Gatis *et al.* 2016), where blocking of ditches results in a rise in the water table successful recolonization by blanket bog vegetation is likely (Haapalehto *et al.* 2010; D'Astous *et al.* 2013Menberu *et al.* 2016), and the process of succession can be rapid with notable change within the one or two years following restoration (Komulainen *et al.* 1999; Tuittila *et al.* 2000). The speed of recovery is likely due to numerous factors, such as existing seed or propagule bank and nutrient availability, with minerotrophic fens seemingly showing a faster recovery than ombrotrophic mire (Komulainen *et al.* 1999; Jauhiainen *et al.* 2002). The successional community will also depend on these factors, and geographically close sites may produce notably different vegetation assemblages if there are differences in nutrient availability or topography (Timmermann *et al.* 2006; Kozlov *et al.* 2016).

Reintroduction of peatland species has also been suggested as a means of speeding the process of regeneration. For example, addition of *Sphagnum* spp. has been successfully used as a means of increasing diversity of this crucial group in rewetted bogs, which may otherwise support a fairly species-poor community in the period following restoration (Robroek *et al.* 2009). However, the success of this technique is likely site and species dependent, with translocation of vascular plants reportedly more successful than translocation of bryophytes (Rochefort *et al.* 2016).

While numerous studies demonstrate the positive effects of rewetting, it is also reported that regenerating communities are not identical to those of pristine, reference peatlands (Lavoie & Rochefort 1996; D'Astous *et al.* 2013; Rochefort *et al.* 2016). While this may be expected in the short term, some relatively long-term studies have reported the same effect, with regenerating mire lacking the presence of certain indicators of pristine bog 10 years after restoration (Haapalehto *et al.* 2011). These results highlight the slow recovery time of blanket bog communities, and while it may be the case that bogs would revert

to a pristine state with sufficient time following restoration, it is also possible that drainage and harvesting have caused permanent change in mire communities. While the level of success is highly situation dependent, it is clear that restoration will result in some form of vegetation change. These changes may be fairly subtle, but where rewetting is accompanied by a rise in the water table succession towards mire vegetation communities can be expected, with an associated decrease in cover of species favouring drier conditions.

3.1.4 Nutritional quality of plants

Numerous different measures affect the nutritional value of a plant; Table 8 provides definitions for some of the most important contributors to quality. The percentage of dry matter in a plant refers to the weight of all constituents once water has been removed. However, dry matter alone cannot be used as an indicator of quality, and if the dry matter is largely composed of fibrous, cell wall components its value decreases (Oliveira *et al.* 2011). The fibrous content of a sward is typically measured as either the percentage of acid detergent fibre (ADF), which includes lignin and cellulose, or neutral detergent fibre (NDF), which includes hemicellulose in addition to the two previous components. While fibre is an essential part of the diet, high levels result in a lower quality of sward as these components are highly indigestible. As a result, levels of ADF and NDF provide an accurate estimation of voluntary intake of a forage by livestock (Stensig *et al.* 1994; Allen 1996), with higher levels of fibre resulting in decreased levels of intake. Essentially, higher levels of fibre will provide fill, thereby reducing the interest in further feeding, without providing nutrition due to the animal's inability to digest it. Therefore, animals using forages with excessively high levels of ADF and NDF will show reduced performance, through decreased milk production for example (Beauchemin 1991; Munoz *et al.* 2016).

Digestibility and metabolisable energy are inversely related to proportions of NDF and ADF, and as a result increased digestibility results in improved animal performance (Duble *et al.* 1971; Mayombo *et al.* 1997). Both measures relate to the proportion of dry matter which is digestible; primarily the non-fibrous components, along with some digestible cell wall components. The percentage

digestibility refers to the proportion of dry matter which can be digested, whereas the metabolisable energy is the amount of energy that can be obtained from these digestible components (Table 8). As a result, the two measures are closely linked, with a higher digestibility resulting in higher levels of metabolisable energy. High values for these measures reflect a high-quality sward, as a highly digestible sward will allow improved nutrient uptake by animals and thereby improve performance through, for example, increased milk yield (Holmes *et al.* 1992; Hoogendoorn *et al.* 1992).

Table 8: definitions of some commonly used measures of plant nutritional quality, adapted from Saha *et al.* 2013.

Measure	Definition
Crude Protein (CP)	The total nitrogen (N) in the diet, including both true protein and also non-protein nitrogen
Digestibility (D)	The extent to which the feed is absorbed by an animal as it passes through the digestive system
Dry Matter (DM)	All non-water components of the feed, measured as the total weight of the feed with water removed
Metabolisable Energy (ME)	The gross feed energy minus the energy lost through excretion
Neutral Detergent Fibre (NDF)	A measure of plant cell wall components and total fibre constituents, including cellulose, hemicellulose, lignin, silica, tannins and cutins.

Crude protein is another indicator of sward quality, with higher levels reflecting a higher quality sward. Protein is required for gaining muscle mass, and therefore higher levels of crude protein in a sward are associated with higher rates of weight gain (Gleghorn *et al.* 2004; Boland *et al.* 2013). The combination of a high proportion of crude protein and a high digestibility, or metabolisable energy, is seen as particularly indicative of high-quality, and these are the measures used to calculate the relative feed quality of a forage (Saha *et al.* 2013).

One perhaps more obvious component of plant nutritional value is the presence of toxins. Ingestion of toxic plant species can result in a decline in health and occasionally mortality depending on the severity of the poisoning, and where common this can have a significant impact on the agricultural industry (James *et al.* 1992a; James *et al.* 1992b). However, the effect of harmful components may vary greatly; for example, although tannins may cause toxicity in some cases, in other situations they may improve livestock performance (Wang *et al.* 1996; Makkar 2003).

Nutritional quality varies within individual plants, with leaves typically being significantly more digestible than stems (Terry & Tilley 1964; Albrecht *et al.* 1987). Furthermore, the growing environment will have an effect forage quality, and intra-specific differences can occur when individuals of the same species are grown under different conditions (Seguin *et al.* 2002). Annual species exhibit seasonal variation in quality, typically showing a decline in measures of quality such as protein and digestibility from spring to autumn due to maturation resulting in an increased proportion of cell wall components in the plant (Machado *et al.* 2004). Generally, both increased water levels and increased temperatures during growth result in a decrease in digestibility of a plant as they promote faster maturation, and as a result increase the proportion of fibrous cell wall components (Buxton 1996). Due to the influence of environmental conditions on nutritional quality, there is potential for weather patterns to alter the nutritional value of vegetation within and between years (Seligman & Sinclair 1995; Lenart *et al.* 2002).

Different plant species differ in their nutritional content (Freer & Jones 1984; Seguin *et al.* 2002). Comparison of species has often focussed on the differences in those species most frequently sown for grazing, such as perennial ryegrass *Lolium perenne* and white clover *Trifolium repens* (Beever *et al.* 1985; Beever *et al.* 1986) and alfalfa *Medicago sativa* in American pastures (Warren *et al.* 1974). In intensively managed lowland pastures species mixes can be closely controlled through seeding, and application of fertiliser. As a result, management of swards allows the establishment of productive species mixes to maximise animal performance, with a selected proportion of grasses for dry matter production and longer growing season combined with legumes such as white clover to increase digestibility (Frame & Newbould 1986). However, a substantial portion of grazing land lies outside of these intensively-managed systems in semi-natural pastures, where available forage may consist of a diversity of native plant species. Studies have attempted to compare the relative value of naturally occurring forage species (Mautz *et al.* 1976; Pontes *et al.* 2007), but these have received less research than those species used in the pastures of intensive farming. Nevertheless, the work that has been done on forage quality of semi-natural pastures, along with the information on drivers of variability in the value of intensive pastures, suggests that the quality of grazing in semi-natural and natural habitats is likely to vary greatly depending on factors such as species diversity of the sward, and environmental conditions.

3.1.5 Nutritional quality of upland pastures

The nutritional value of moorland plants can be affected by numerous factors. Seasonality appears to be important, with a decline in the digestibility of swards from spring through to autumn with maturation (Grant & Campbell 1978; Hodgson *et al.* 1991). While grazing regime may affect the physical structure of a sward, the impact of this on quality is variable among species. For example, a closely grazed *Nardus* sward has lower digestibility than a longer sward (Common *et al.* 1998), whereas the digestibility of *Molinia*-dominated swards does not appear to be significantly affected by grazing regime (Common *et al.* 1997).

The quality of individual species has received relatively little study, but *Molinia* has been noted as containing high levels of crude protein (Thomas & Ibbotson 1947). Additionally, a study of blanket bog species noted relatively high levels of digestibility for the spring growth of most species (Grant & Campbell 1978), and analysis of hay from moorland plant communities has suggested that intake potential should be fairly high due to the high digestibility (Armstong *et al.* 1986). Among moorland communities, digestibility and animal performance are typically higher in grass communities than in those dominated by dwarf shrubs (Hodgson *et al.* 1991), and among typical moorland grass communities *Agrostis/Festuca* swards offer higher digestibility than those dominated by *Molinia* or *Nardus* (Common *et al.* 1991).

A number of studies have examined the quality of semi-natural hill grassland swards in comparison with improved permanent pastures. Improved pastures, such as mixtures of *Lolium perenne* and *Trifolium repens*, have higher digestibility and higher levels of crude protein than semi-natural grasslands, including those dominated by *Agrostis/Festuca*, *Molinia*, and *Nardus* (Davies 1987; Common *et al.* 1991; Hodgson *et al.* 1991). This is reflected in animal performance, with both sheep and cattle showing improved live weight gain and growth in permanent pastures when compared to semi-natural grasslands (Common *et al.* 1991; Fraser *et al.* 2007; Fraser *et al.* 2009; Fraser *et al.* 2013). As a result, liming and seeding moorland pastures with a mixture of *Lolium* and *Trifolium* is an effective means of improving digestibility and animal live weight gain, although the creation and maintenance of these swards are challenging in upland environments (Copeman 1978).

Nevertheless, despite the relatively low animal performance on semi-improved pastures, moorland plant communities have been noted to offer acceptable weight gains (Common *et al.* 1997; Fraser *et al.* 2013), demonstrating that they do have some utility for grazing. *Calluna* and *Molinia*-dominated communities are able to offer acceptable levels of weight gain in both sheep and cattle (Critchley *et al.* 2008). *Nardus* dominated swards may provide suitable grazing depending on the presence, and height, of other species, but tightly grazed swards can result in negative weight gain and are therefore unsuitable for grazing by cattle (Common *et al.* 1998).

While it is perhaps not unexpected that semi-natural moorland swards are of a lower quality than cultivated pastures, they are clearly able to offer some grazing value.

3.1.6 Hypotheses

This study aimed to address two questions:

1. Do different upland habitats differ in terms of grazing value?

2. How will peatland restoration affect the grazing value of upland pastures?

Data on the nutritional quality of different moorland plant species were obtained by collecting individual species samples and analysing them for quality measures including dry matter, neutral detergent fibre, digestibility, metabolisable energy and crude protein. This allowed an examination of seasonal variation in the quality of different plant species, by comparing the nutritional quality of single species samples collected in spring and autumn.

In order to estimate the nutritional quality available in different moorland habitats, the plant species composition of different vegetation communities was recorded, and used to create an estimated value for different sward quality measures based on the percentage cover and quality of different species in each community. It is hypothesised that variation in the plant species compositions of different upland habitats will result in differences in their nutritional quality. Furthermore, it is hypothesised that peatland restoration will negatively alter the grazing value of upland pastures, as changing hydrology may lead to an increase in dwarf shrubs of low nutritional quality.

3.2 Materials and methods

The study was carried out at the Squallacombe and Aclands site (description in Chapter 2.2.1), which was selected for its representative range of Exmoor's common moorland habitats. The site is grazed by ca. 40 Red Devon Cattle from midsummer to early autumn (June – October) each year. Small numbers of sheep are also present intermittently, while herds of wild red deer occur year round.

3.2.1 Vegetation surveys

Pilot Study

A pilot study attempted to determine whether sward quality differed adjacent to blocked and unblocked drainage ditches, and whether quality varied with distance from a drainage ditch. Sward samples were collected from set quadrats along transects that stretched from 1 to 6 metres away from ditches. This work was carried out at Aclands and Spooners, with six transects at each site. Following restoration, some ditches were left unblocked at these sites to act as controls, and transects were located in pairs: one adjacent to an unblocked ditch, and one adjacent to the nearest blocked ditch. Transects ran at a 90° angle to the ditch, and downslope from it. Transects measured 6m long by 3m wide, each of the six quadrats being 1m by 3m.

Sward sampling was carried out in Autumn 2012 and Spring 2013 as part of the pilot study, and I continued this work in Autumn 2013, Spring 2014, Summer 2014, and Autumn 2015. Sampling involved the collection of approximately 400g of a representative mixture of vegetation from quadrats. In Autumn 2012, and Spring 2013, samples were taken from every quadrat (a total of 72 samples per sampling day), all on the same day. Samples were sent out by courier on the next day for analysis by an external company (described fully below). In the remaining three sampling seasons, the number of samples taken was reduced due to the cost of laboratory analysis. The sampling strategy varied between sampling seasons. In Autumn 2013, samples were collected from all quadrats at Spooners (n = 36), and one representative sample per transects was collected from Aclands (n = 6). The more intensive sampling effort at Spooners reflected the fact that it had recently been restored. In Spring and Summer 2014 the focus of the monitoring effort switched to Aclands, and samples were collected from all quadrats there (n = 36 in each sampling season), while an average per transect was collected at Spooners (n = 6 per season). Finally, in Autumn 2015, in an effort to detect the effects of drainage ditches on quality while reducing costs, one sample per two quadrats was taken from each transect (n = 3 per transect, 18 per site) at both Spooners and Aclands.

Results from this study are provided in Appendix 1. No significant differences in sward quality were found between sites or between blocked and unblocked drainage ditches, and there was no significant effect of distance from a ditch on sward quality. Results were highly variable, and inconsistent between years. It is likely that differences in sward quality may not manifest themselves at such fine a scale, particularly as ditch blocking appears to have a variable and unpredictable impact on the depth of the water table in the close proximity of the ditch (Luscombe *et al.* 2016). Differences between years could be due to weather conditions in the period preceding sampling. Based on the findings of this study, it was decided to change the approach to sampling to instead measure the quality of individual moorland plant species, instead of focussing on quality in relation to drainage features. As the expected outcome of rewetting is a change in species composition, and this will be used to measure the success of restoration, ascertaining the quality of individual species was deemed to be a more informative method of predicting changes in sward quality.

Selection of Study Species

The nutritional quality of moorland plant species was analysed in order to determine how changes in their prevalence may affect a site's grazing value, and to estimate the quality of different habitats based on species composition. The selected species meet two criteria: they are present at high frequency in one or more of the site's habitats, and are used by cattle for grazing. The first criteria was judged from walkover surveys of the site, as well as previous vegetation surveys carried out as part of the Exmoor Mires Project. The second criteria was primarily judged by direct observation of cattle grazing behaviour on the site, but was supplemented by studies on cattle diet from the literature (Grant *et al.* 1985; Grant *et al.* 1987). Certain species were included despite occurring at low density as they appeared to be actively selected by cattle where present. For example, *Carex binervis* comprises a relatively small proportion of the sward in drier grassland habitats, but is heavily grazed wherever present (pers. obs.) and is therefore likely to contribute a disproportionately large amount to cattle diet relative to its frequency. In contrast, some species common in certain habitats were excluded if they were

unlikely to contribute to cattle diet, for example due to unpalatability of the species, as in bracken, or inaccessibility of the habitat, as in *Carex rostrata*. Due to the limited ability of cattle to show fine-scale selection of forage species (Grant *et al.* 1985), bryophytes were grouped based on habitat as it was deemed unlikely that cattle would be able to select from within low-growing mats containing numerous species. 'Turf mosses', included common grassland species such as *Hypnum cupressiforme*, *Rhytidiadelphus squarrosus* and *Pleurozium schreberi*, while the *Sphagnum* group included *S. cuspidatum, S. fallax, S. papillosum and S. subnitens*. The full list of sampled species, along with the justification for their inclusion, is provided in Table 9.

Species Composition of different habitats

Surveys to record plant species composition in the different habitat types were carried out in September 2016. Descriptions of different habitat categories, along with their distribution on the site, are given in Chapter 2.2.2. Within each habitat one representative 2m x 2m quadrat was selected. The location was chosen after having walked through a habitat patch to gain an understanding of the abundance and distribution of different species, with squares being selected to contain a representative mix and cover of species reflecting their abundance in the habitat patch as a whole. A description of how habitats were divided by category is given in Chapter 2.2.2. In each 2m x 2m square, plants and bryophytes were recorded along with an estimate of their percentage cover. The surveys were not intended to be exhaustive, but instead to gather an estimate of the differing proportions of the common moorland species in different habitats. With this in mind, there was a focus on the species (or species aggregates) selected for nutritional quality analysis, but any other frequent species were also recorded. It is inevitable that some of the scarcer, more inconspicuous species will have been overlooked, but as these occur at extremely low densities it is likely that they will make a negligible contribution to the overall quality of the sward.

Sample Collection

Samples were collected on two dates to provide values for nutritional quality at different times of year. Sampling was first carried out in September 2015, and then again in June 2016. In 2015, 19 samples were collected. This included single samples of 16 species (or species groups), as well as 3 separate *Molinia caerulea* samples. Repeat *M. caerulea* samples were taken in an attempt to identify variability in the nutritional quality of a species when it is growing in different habitats, in order to provide an indication of the level of caution required when interpreting the results. *Molinia* was selected due to its abundance, and its presence in a variety of different habitat types. Samples were taken from dry grassland, *Molinia*-dominated grassland, and transitional bog habitats. In 2016, the same 19 samples were collected along with an additional 5 individual species samples, which were included to facilitate an analysis of the nutritional quality of different habitats. Analysis of a large number of samples would have been prohibitively expensive, so instead, an attempt was made to produce a single representative sample for each species by ensuring that it was comprised of a large number of individual plants. Each species sample was made up of a number of different individual plants, and plants were collected from a minimum of three locations within every different habitat category that the species was present. The number of individual plants from which material was collected depended on the abundance and physical characteristics of the species, but each sample contained cuttings from a minimum of 10 individual plants. Plants were identified in the field and sorted in to individual species bags. Collection involved cutting plant matter using scissors and removing any dead material and pieces of non-target species. For vascular plants, effort was made to obtain a representative blend of leaf, stem, and flower/seed head components. Approximately 400g of plant matter was collected for each sample.

3.2.2 Nutritional analysis

Samples were sent for external analysis, carried out by Yara Analytical Services (York, UK). Yara is a company specialising in analysis of plant and soil samples to help inform agricultural practices. Samples were picked up by courier the day

after being collected in the field. “Feed Value Fresh Grass (L4c)” analysis was carried out on the samples, providing values for dry matter, crude protein, neutral detergent fibre (NDF), metabolisable energy, and digestibility. The methods used here represent industry standards (Thomas 1990; Mariotti *et al.* 2008), and are therefore used to allow comparison with quality values for other forage types. Dry matter content is measured by weighing a sample then drying until all moisture is removed before reweighing. Dry matter is then be expressed as a percentage of the total weight of the sample. Crude protein is estimated from the quantity of Nitrogen in the dry matter portion of a sample. The sample is ground, digested in acid and then distilled in a base solution to produce ammonia. Ammonia is measured, and the quantity of Nitrogen multiplied by 6.25 to reflect the average nitrogen content of biological proteins. NDF is measured by placing a sample in detergent to dissolve non-fibrous components of the dry matter, allowing the remaining fibrous components to be measured. Digestibility is calculated by digesting dry matter *in-vitro,* and then comparing the results against forage with known *in-vivo* digestibility values in order to provide an estimate of *in-vivo* digestibility. Metabolisable energy is estimated from measures of digestibility, using a standard calculation of 0.16 x the percentage digestibility.

Table 9: species selected for nutritional quality analysis. Occurrence provides an estimate of cover in different habitat categories, and codes are: BD = bracken-dominated; DG = dry grassland; RD = rush-dominated; VM = valley mire & flushes; MD = *Molinia*-dominated; TB = transitional bog; BB = blanket bog. Colours represent the following:

absent | 0-5% cover | 5-20% cover | 20-50% cover | >50% cover

Name	Scientific Name	Type	Ellenberg F Value	Occurrence							Grazing Use
				BD	DG	RD	VM	MD	TB	BB	
Bents	*Agrostis* spp.	Graminoid	5-7								Evidence on site, Grant *et al.* 1985
Sweet Vernal	*Anthoxanthum odoratum*	Graminoid	6								Evidence on site, Grant *et al.* 1985
Heather	*Calluna vulgaris*	Dwarf-shrub	6								Grant *et al.* 1987
Green-ribbed Sedge	*Carex binervis*	Graminoid	6								Evidence on site
Heath Grass	*Danthonia decumbens*	Graminoid	6								Evidence on site
Tufted Hair-grass	*Deschampsia cespitosa*	Graminoid	6								Evidence on site, Grant *et al.* 1985
Wavy hair-grass	*Deschampsia flexuosa*	Graminoid	5								Evidence on site, Grant *et al.* 1985
Cross-leaved Heath	*Erica tetralix*	Dwarf-shrub	8								Grant *et al.* 1987
Common Cottongrass	*Eriophorum angustifolium*	Graminoid	9								Grant *et al.* 1987
Hares-tail Cottongrass	*Eriophorum vaginatum*	Graminoid	8								Grant *et al.* 1987
Sheep's Fescue	*Festuca ovina*	Graminoid	5								Evidence on site, Grant *et al.* 1985
Heath Bedstraw	*Galium saxatile*	Herb	6								Evidence on site, Grant *et al.* 1987
Yorkshire Fog	*Holcus lanatus*	Graminoid	6								Grant *et al.* 1985
Turf Mosses	Various	Bryophyte	-								Grant *et al.* 1987
Soft Rush	*Juncus effusus*	Graminoid	7								Evidence on site, Grant *et al.* 1987
Purple Moor-grass	*Molinia caerulea*	Graminoid	8								Evidence on site, Grant *et al.* 1987
Mat-grass	*Nardus stricta*	Graminoid	7								Grant *et al.* 1985
Bog Asphodel	*Narthecium ossifragum*	Herb	9								Evidence on site, Grant *et al.* 1987
Tormentil	*Potentilla erecta*	Herb	7								Grant *et al.* 1987
Peat Mosses	*Sphagnum* spp.	Bryophyte	-								Grant *et al.* 1987
Deergrass	*Trichophorum cespitosum*	Graminoid	8								Evidence on site, Grant *et al.* 1987
Bilberry	*Vaccinium myrtillus*	Dwarf-shrub	6								Evidence on site, Grant *et al.* 1987

3.2.3 Statistical analysis

Statistical analysis was carried out on five measures of nutritional quality: dry matter, crude protein, neutral detergent fibre, metabolisable energy and digestibility. To determine whether these measures differed between seasons, a paired t-test was carried out on values of the 17 species that were sampled in both September and June. Ellenberg F Values for moisture (Hill *et al.* 1999), which are used to classify plants based on their association with particular environmental conditions, were used in order to determine whether nutritional quality of species differed based on their preference for different levels of habitat wetness. Vascular plant species were grouped by Ellenberg Value, with the three *Molinia* samples being grouped together to provide a mean value for the species for each measure of quality. A one-way ANOVA was carried out on each measure of quality for both autumn and spring samples in order to identify differences between species with different Ellenberg F Values. Comparison between habitats was based on the categories given in Chapter 2.2.2. Habitat-based comparisons were completed for June only due to the fact that composition of vegetation communities was carried out at this time. The contribution of each species within a community was calculated by multiplying its value for a quality measure by its proportion of the total cover. Each species contribution was then added together to provide an estimate of the overall quality of a vegetation community. Two calculations were made: one including and one excluding the two bryophyte samples. This was done due to the fact that bryophytes frequently comprise a very large proportion of vegetation cover, yet are unlikely to make such a large contribution to livestock diet. Therefore, it was deemed valuable to obtain an estimate of the quality of the vascular plants of each community alone, which make up the more readily available component of a sward. Quality of vegetation communities was grouped by habitat category, and a Kruskal-Wallis one-way analysis of variance was carried out on each measure of quality in order to determine whether different habitat types differed in nutritional quality, both including and excluding bryophytes.

3.2.4 Mapping sward quality

Values for habitat quality were used to produce maps of estimated spatial variability in digestibility and crude protein on the site. These were based on the previously created habitat maps (Chapter 2.2.2). After values were calculated for each different habitat, these were applied to create a site map displaying the percentage digestibility and crude protein in different areas based on vegetation composition. Where a mix of habitats occurred, an intermediate value was calculated based on the measures for the two habitat types. The limitations of this approach are discussed below, but the aim of this work was to provide a broad-scale indication of the spatial pattern of sward quality on the site.

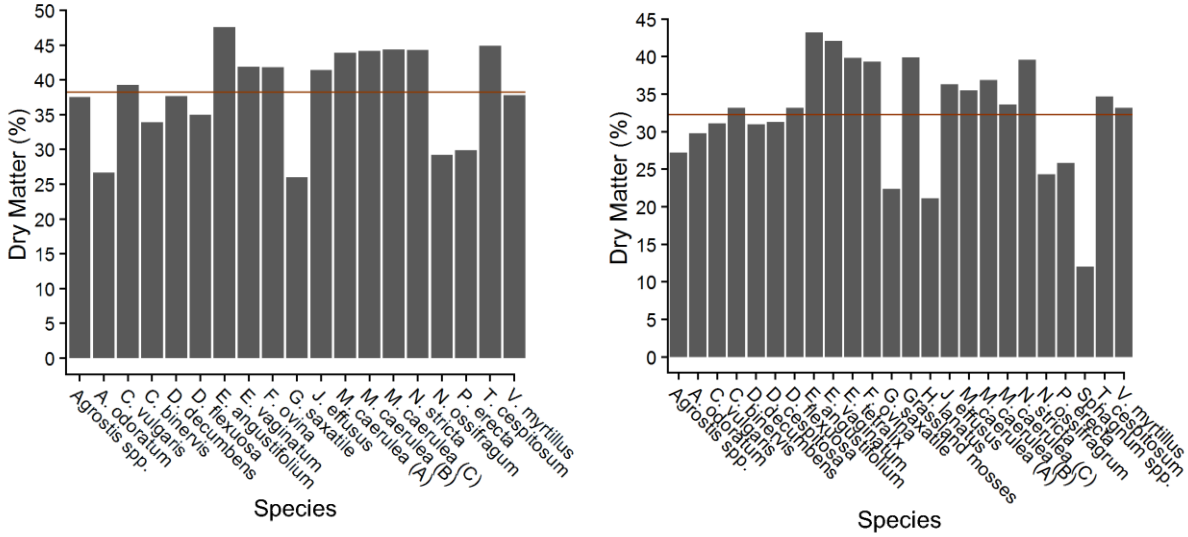


Figure 14: The dry matter content of moorland plant species in autumn (A) and spring (B).

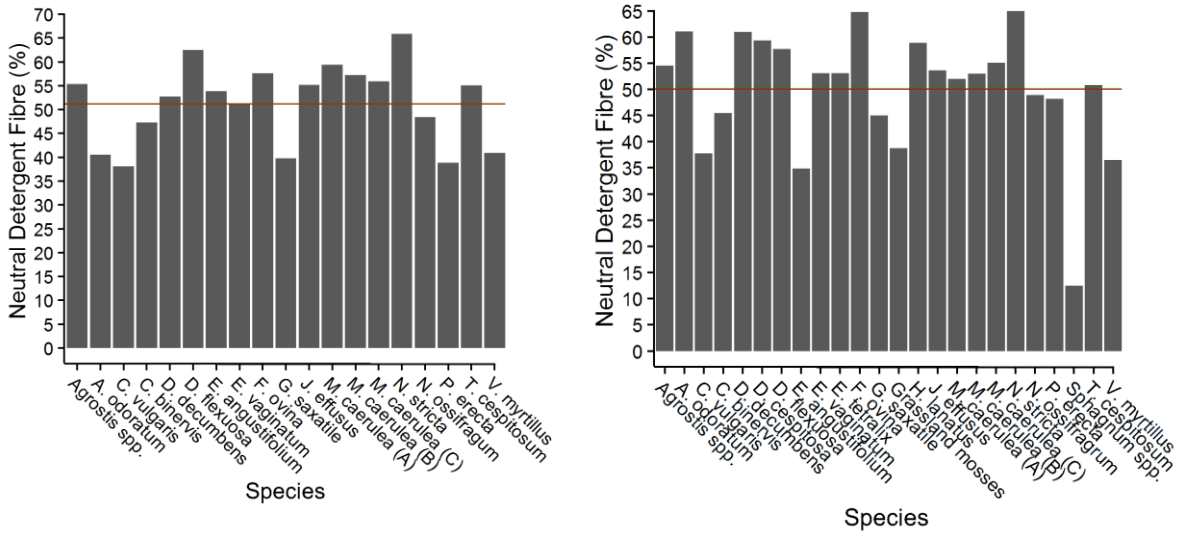


Figure 15: The neutral detergent fibre content of moorland plant species in autumn (A) and spring (B).

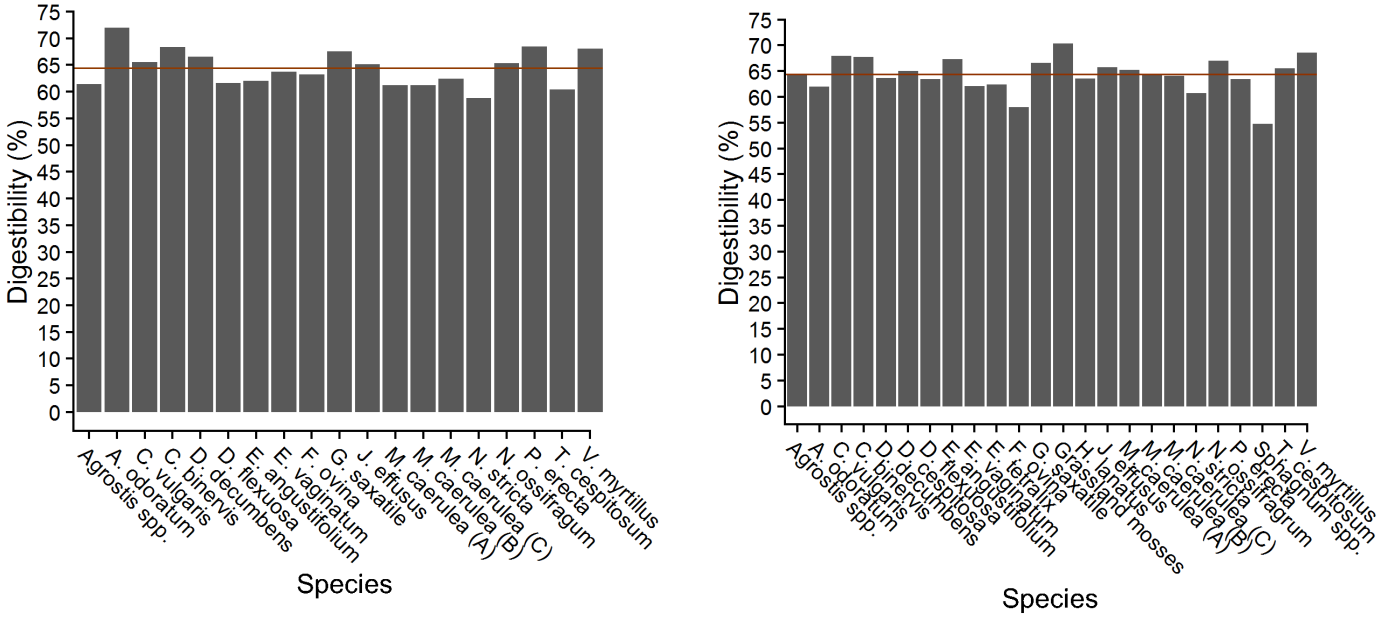


Figure 16: The digestibility of moorland plant species in autumn (A) and spring (B).

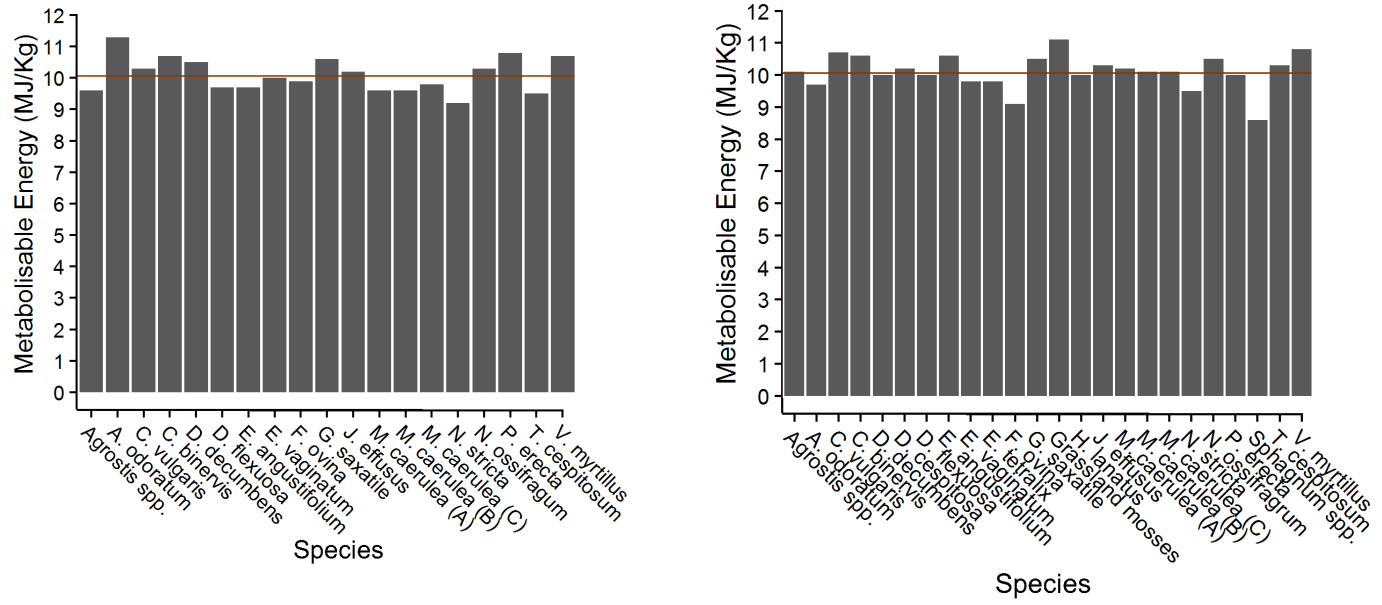


Figure 17: The metabolisable energy of moorland plant species in autumn (A) and spring (B).

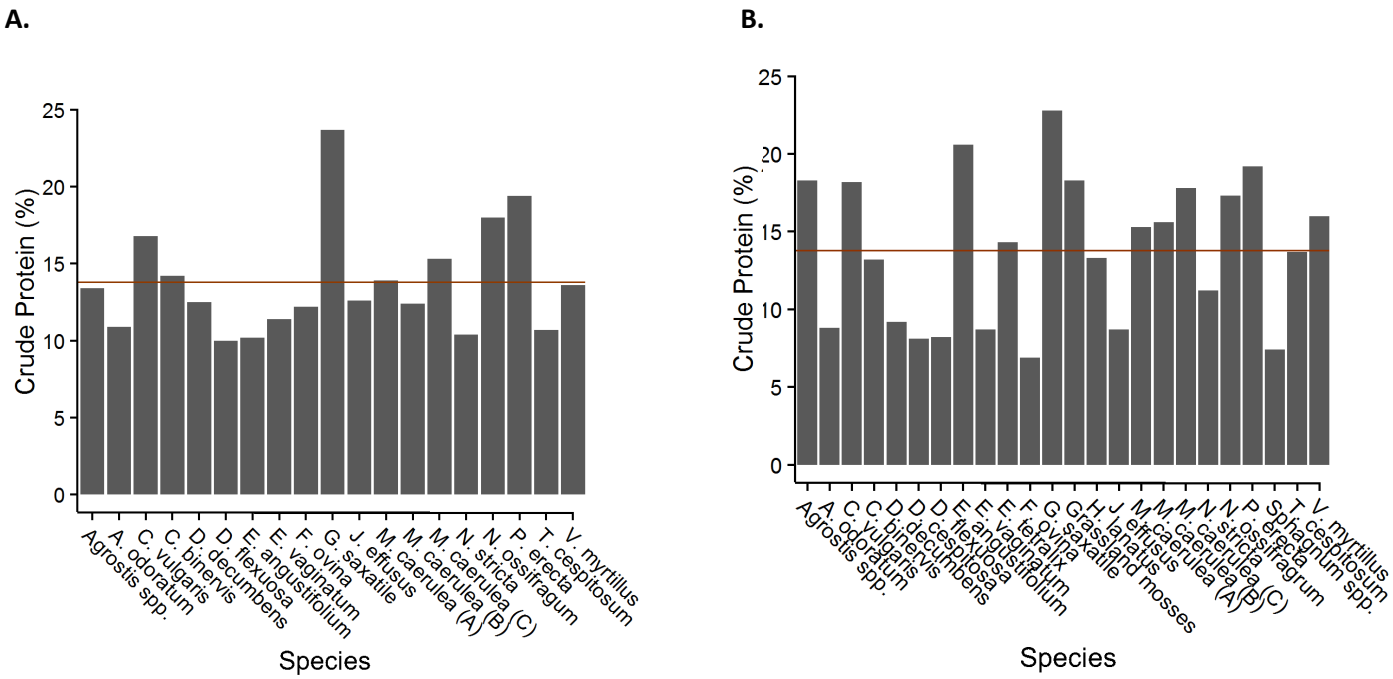


Figure 18: The percentage crude protein of moorland plant species in autumn (A) and spring (B).

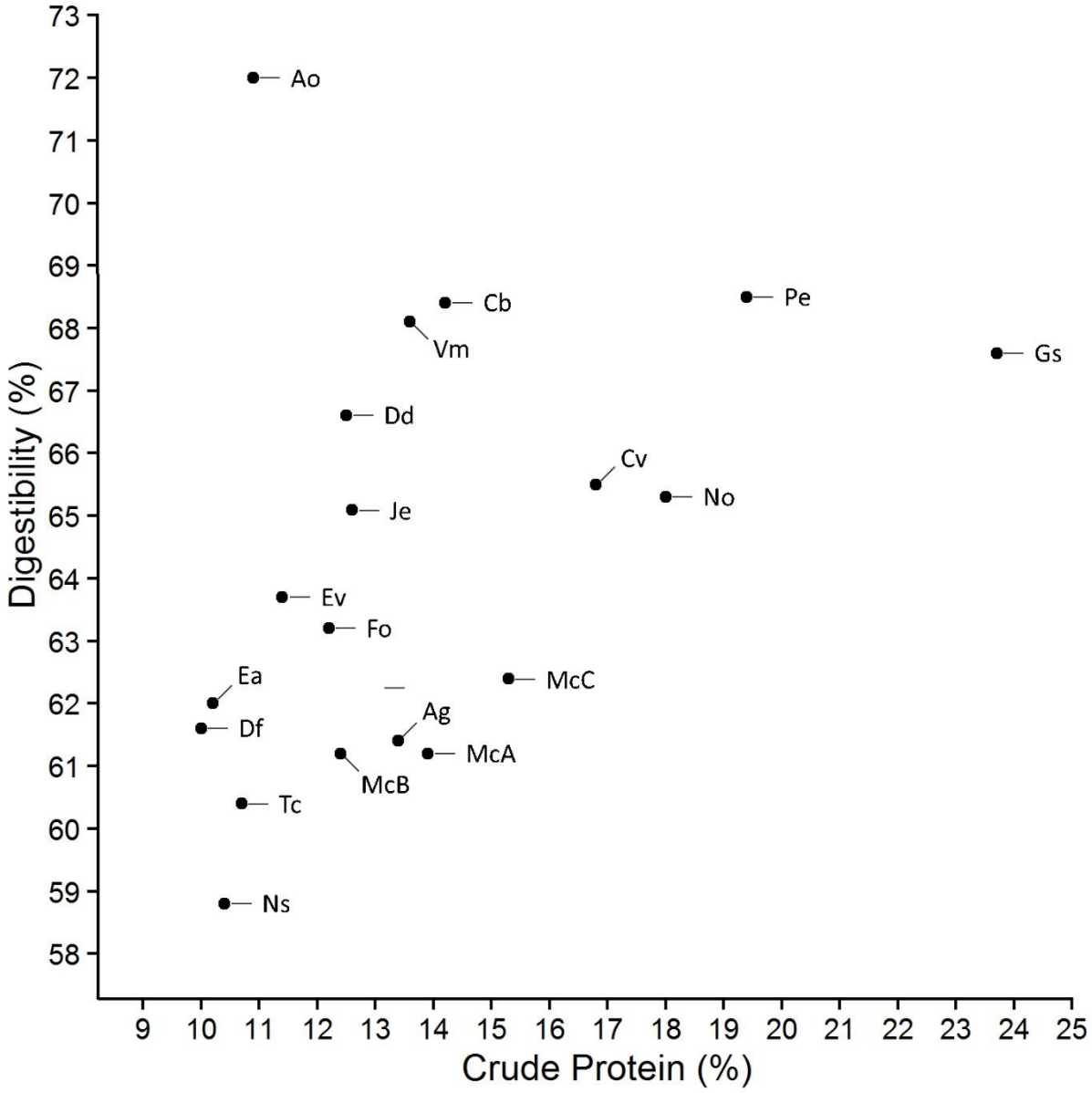


Figure 19: Percentage crude protein and digestibility of moorland plant species from autumn sampling. Species codes are as follows: **Ag** = *Agrostis* spp.; **Ao** = *Anthoxanthum odoratum*; **Cb** = *Carex binervis*; **Cv** = *Calluna vulgaris*; **Dd** = *Danthonia decumbens*; **Df** = *Deschampsia flexuosa*; **Ea** = *Eriophorum angustifolium*; **Ev** = *Eriophorum vaginatum*; **Fo** = *Festuca ovina*; **Gs** = *Galium saxatile*; **Je** = *Juncus effusus*; **McA** = *Molinia caerulea* from dry grassland habitat; **McB** = *Molinia caerulea* from transitional bog habitat; **McC** = *Molinia caerulea* from *Molinia*-dominated habitat; **No** = *Narthecium ossifragum*; **Ns** = *Nardus stricta*; **Pe** = *Potentilla erecta*; **Tc** = *Trichophorum cespitosum*; **Vm** = *Vaccinium myrtillus*.

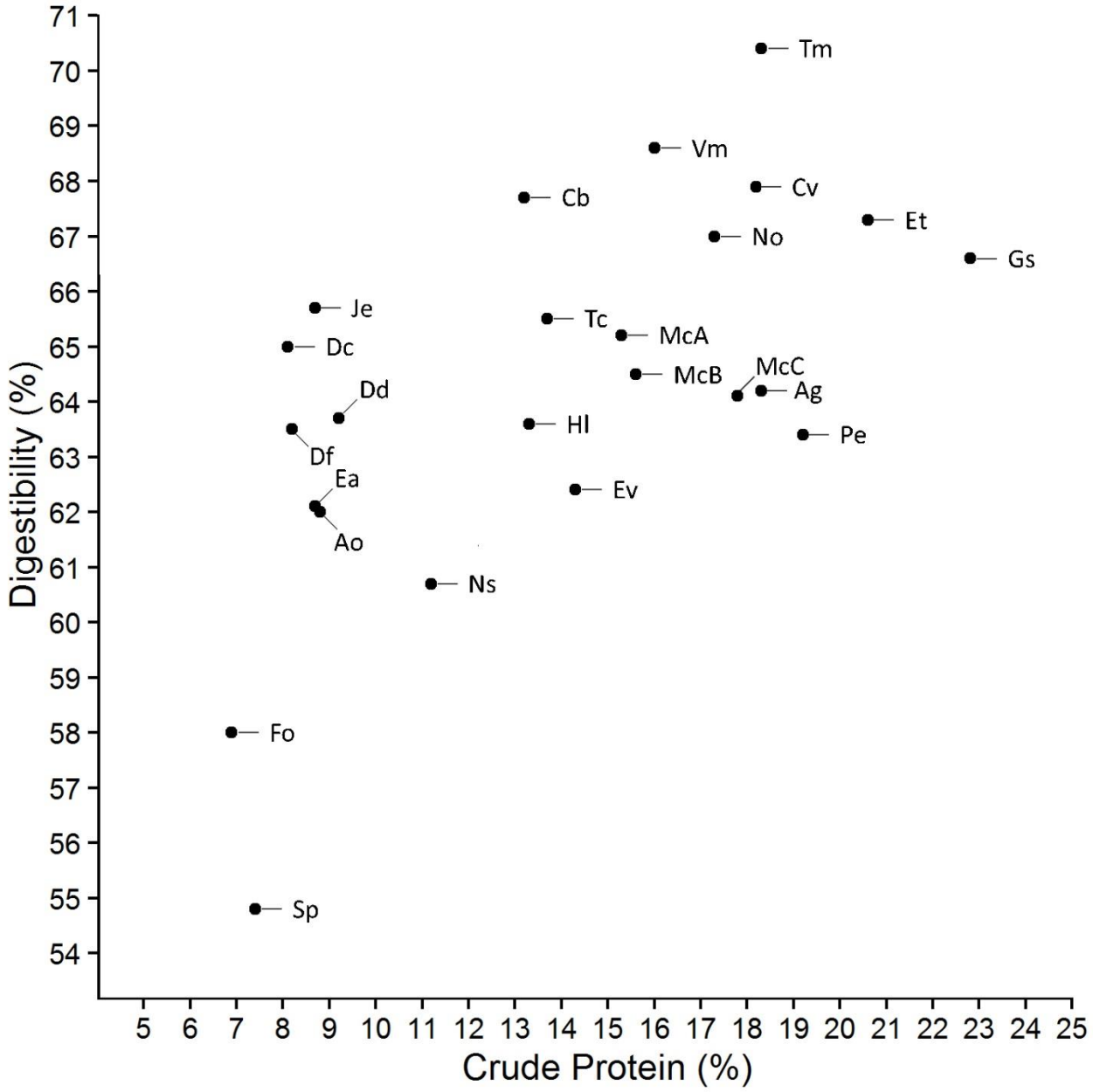


Figure 20: Percentage crude protein and digestibility of moorland plant species from spring sampling. Species codes are as follows: **Ag** = *Agrostis* spp.; **Ao** = *Anthoxanthum odoratum*; **Cb** = *Carex binervis*; **Cv** = *Calluna vulgaris*; **Dc** = *Deschampsia cespitosa*; **Dd** = *Danthonia decumbens*; **Df** = *Deschampsia flexuosa*; **Ea** *Eriophorum angustifolium*; **Et** = *Erica tetralix*; **Ev** = *Eriophorum vaginatum*; **Fo** = *Festuca ovina*; **Gs** = *Galium saxatile*; **Hl** = *Holcus lanatus*; **Je** = *Juncus effusus*; **McA** = *Molinia caerulea* from dry grassland habitat; **McB** = *Molinia caerulea* from transitional bog habitat; **McC** = *Molinia caerulea* from *Molinia*-dominated habitat; **No** = *Narthecium ossifragum*; **Ns** = *Nardus stricta*; **Pe** = *Potentilla erecta*; **Sp** = *Sphagnum* spp.; **Tc** = *Trichophorum cespitosum*; **Tm** = turf mosses; **Vm** = *Vaccinium myrtillus*.

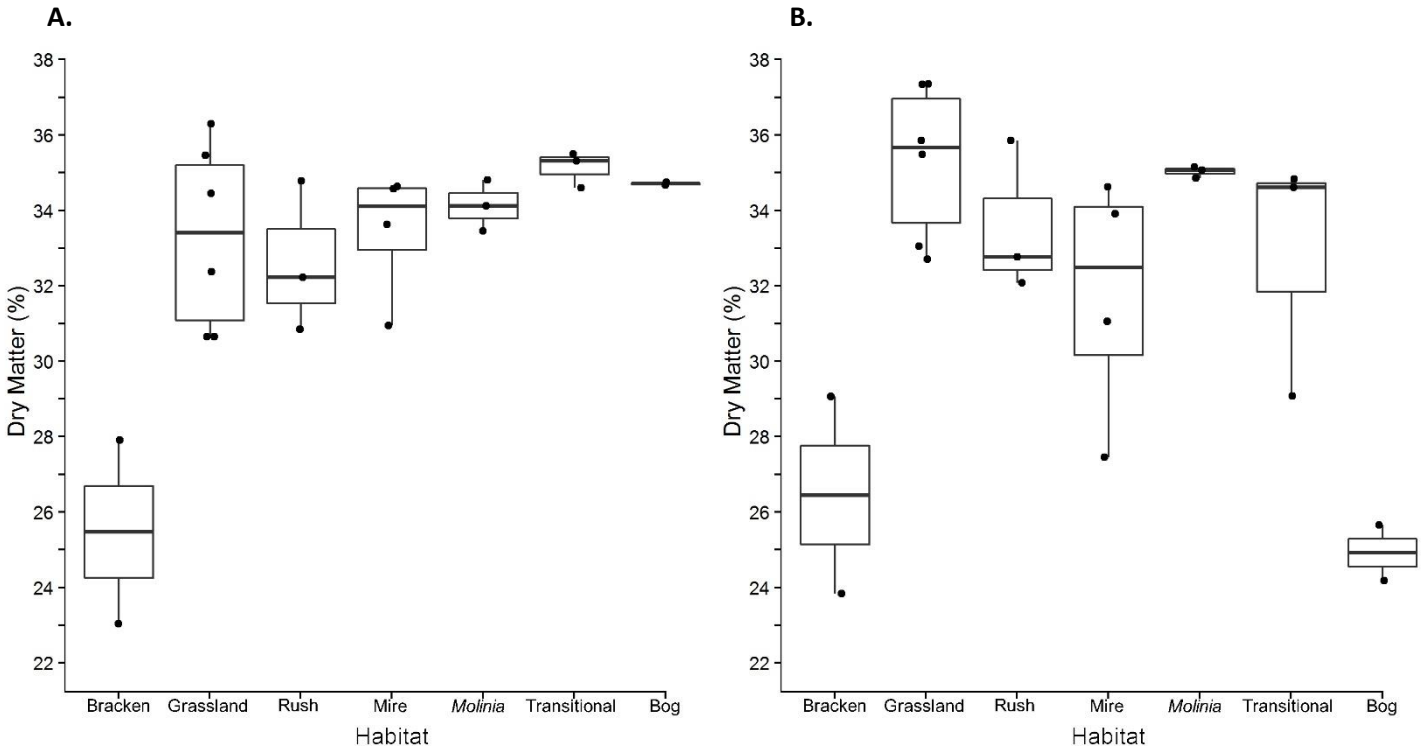


Figure 21: The dry matter content of the vegetation present in different moorland habitats with the exclusion (A) and inclusion (B) of bryophytes. Points represent the estimated dry matter content of the 23 different vegetation communities described in Chapter 2.2.2, based on their species composition. The centre line of the box marks the mean value for each habitat category, while the whiskers show the range.

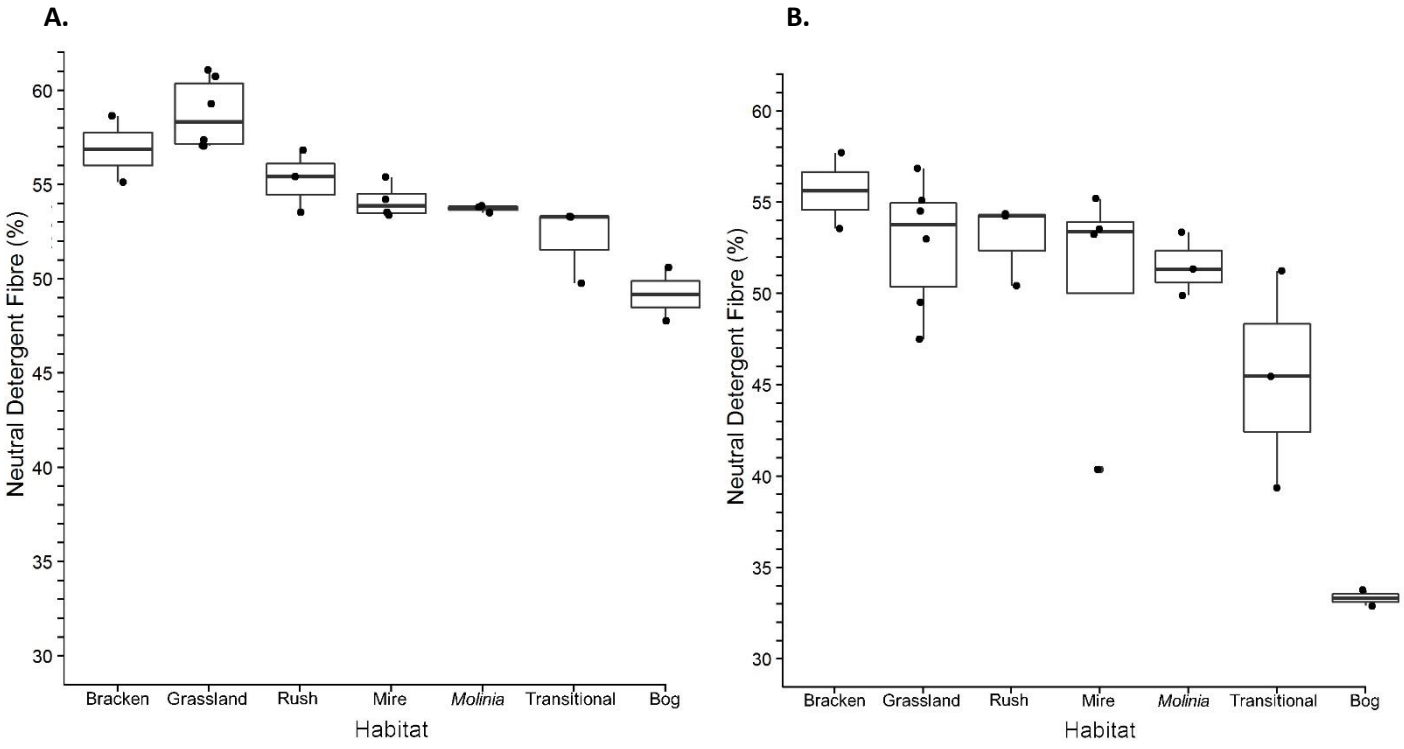


Figure 22: The neutral detergent fibre content of the vegetation present in different moorland habitats with the exclusion (A) and inclusion (B) of bryophytes. Points represent the estimated neutral detergent fibre content of the 23 different vegetation communities described in Chapter 2.2.2, based on their species composition. The centre line of the box marks the mean value for each habitat category, while the whiskers show the range.

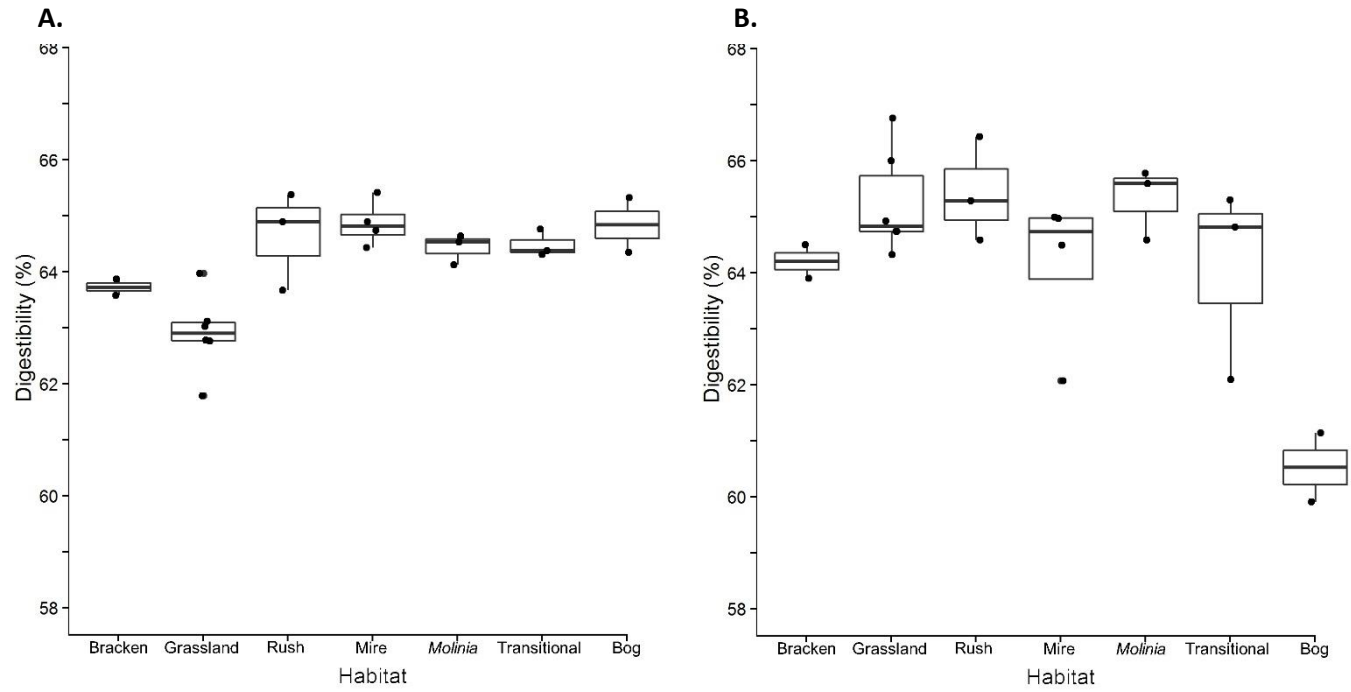


Figure 23: The digestibility of the vegetation present in different moorland habitats with the exclusion (A) and inclusion (B) of bryophytes. Points represent the estimated digtestibility of the 23 different vegetation communities described in Chapter 2.2.2, based on their species composition. The centre line of the box marks the mean value for each habitat category, while the whiskers show the range.

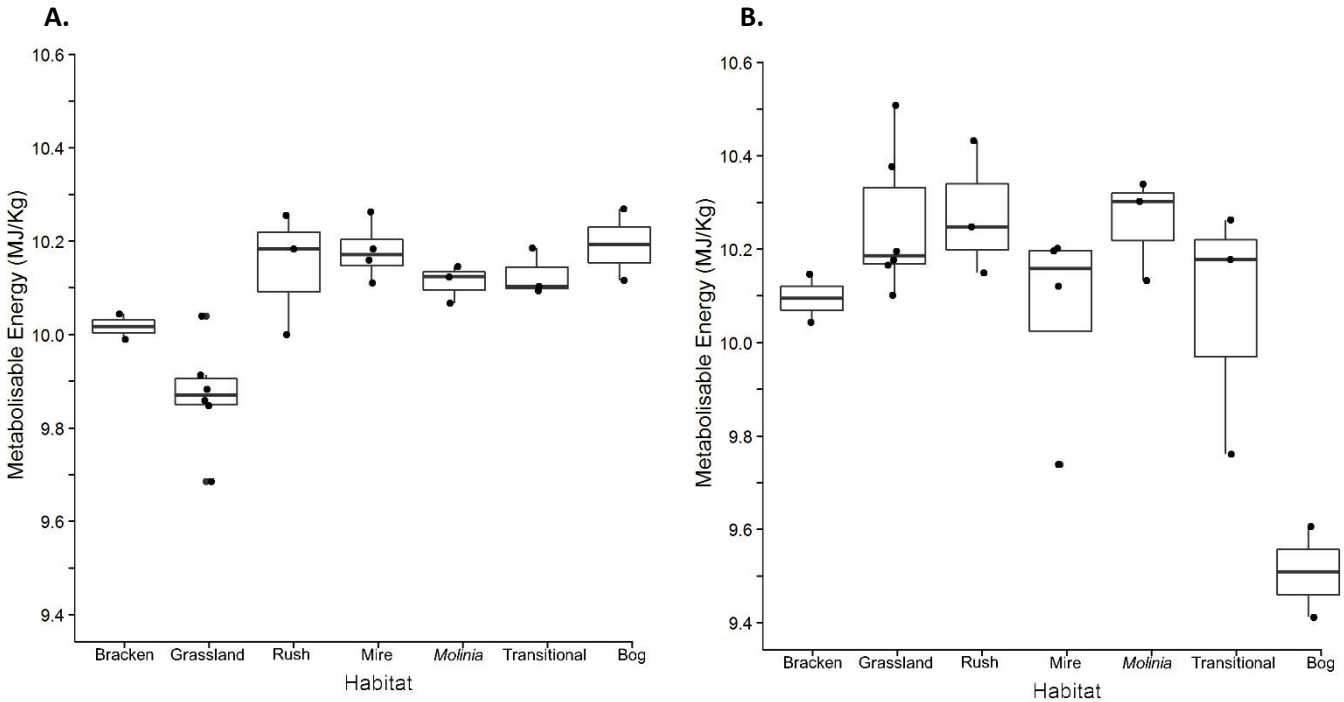


Figure 24: The metabolisable energy of the vegetation present in different moorland habitats with the exclusion (A) and inclusion (B) of bryophytes. Points represent the estimated metabolisable energy of the 23 different vegetation communities described in Chapter 2.2.2, based on their species composition. The centre line of the box marks the mean value for each habitat category, while the whiskers show the range.

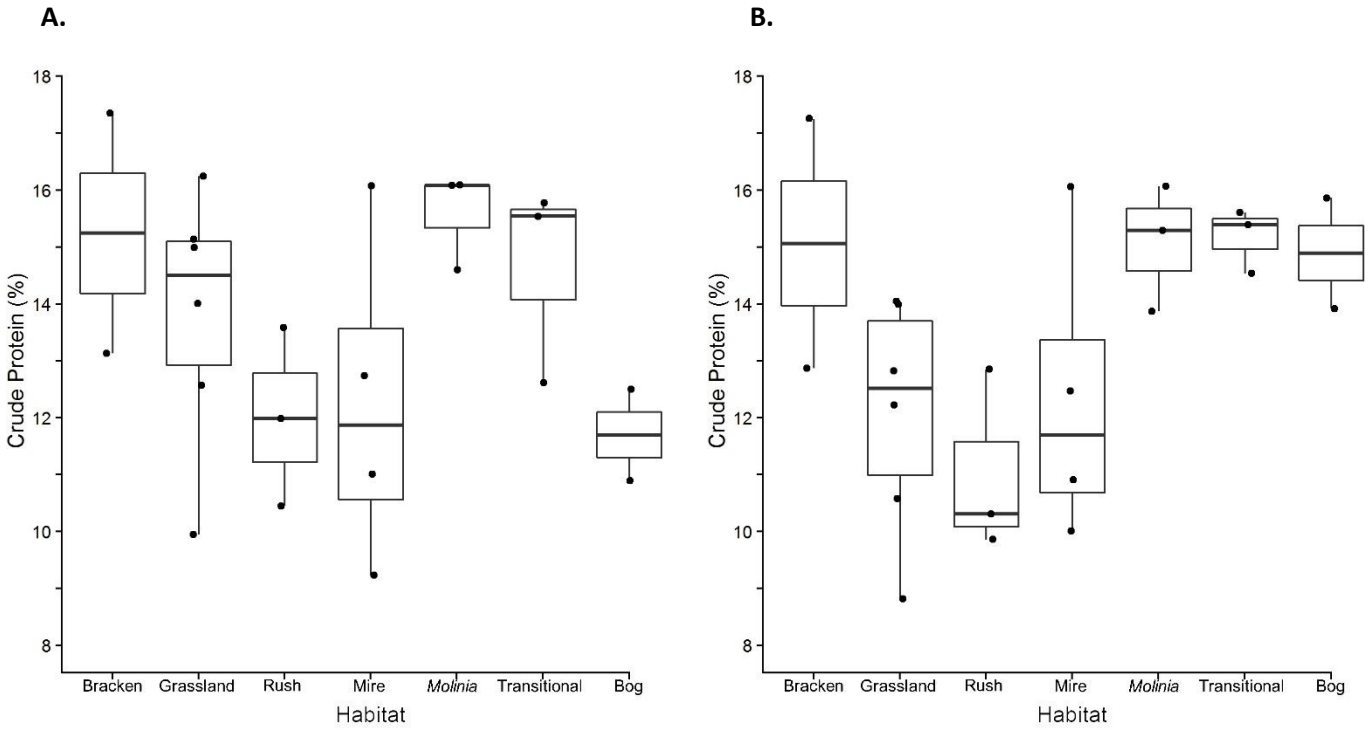
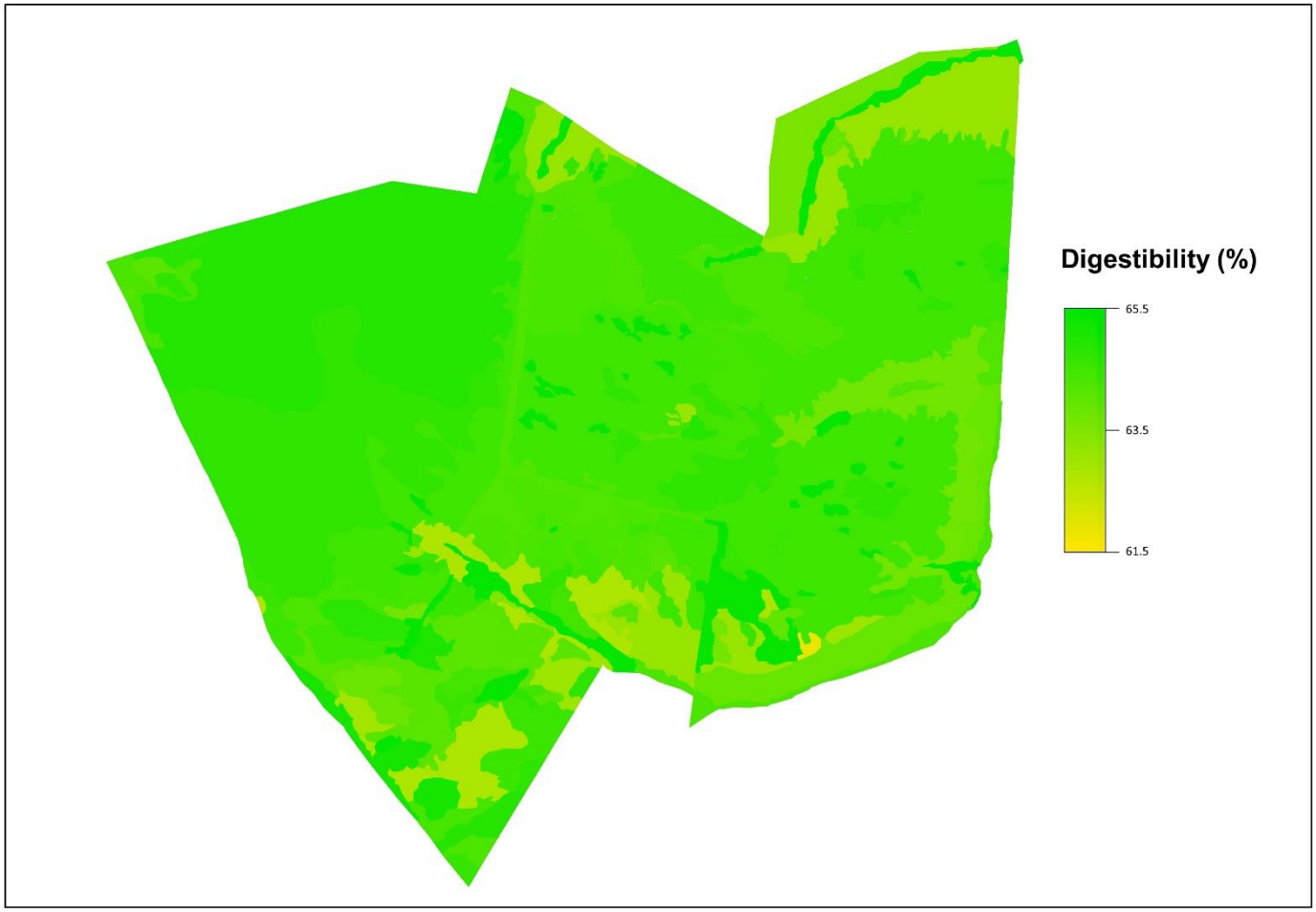


Figure 25: The crude protein content of the vegetation present in different moorland habitats with the exclusion (A) and inclusion (B) of bryophytes. Points represent the estimated crude protein content of the 23 different vegetation communities described in Chapter 2.2.2, based on their species composition. The centre line of the box marks the mean value for each habitat category, while the whiskers show the range.



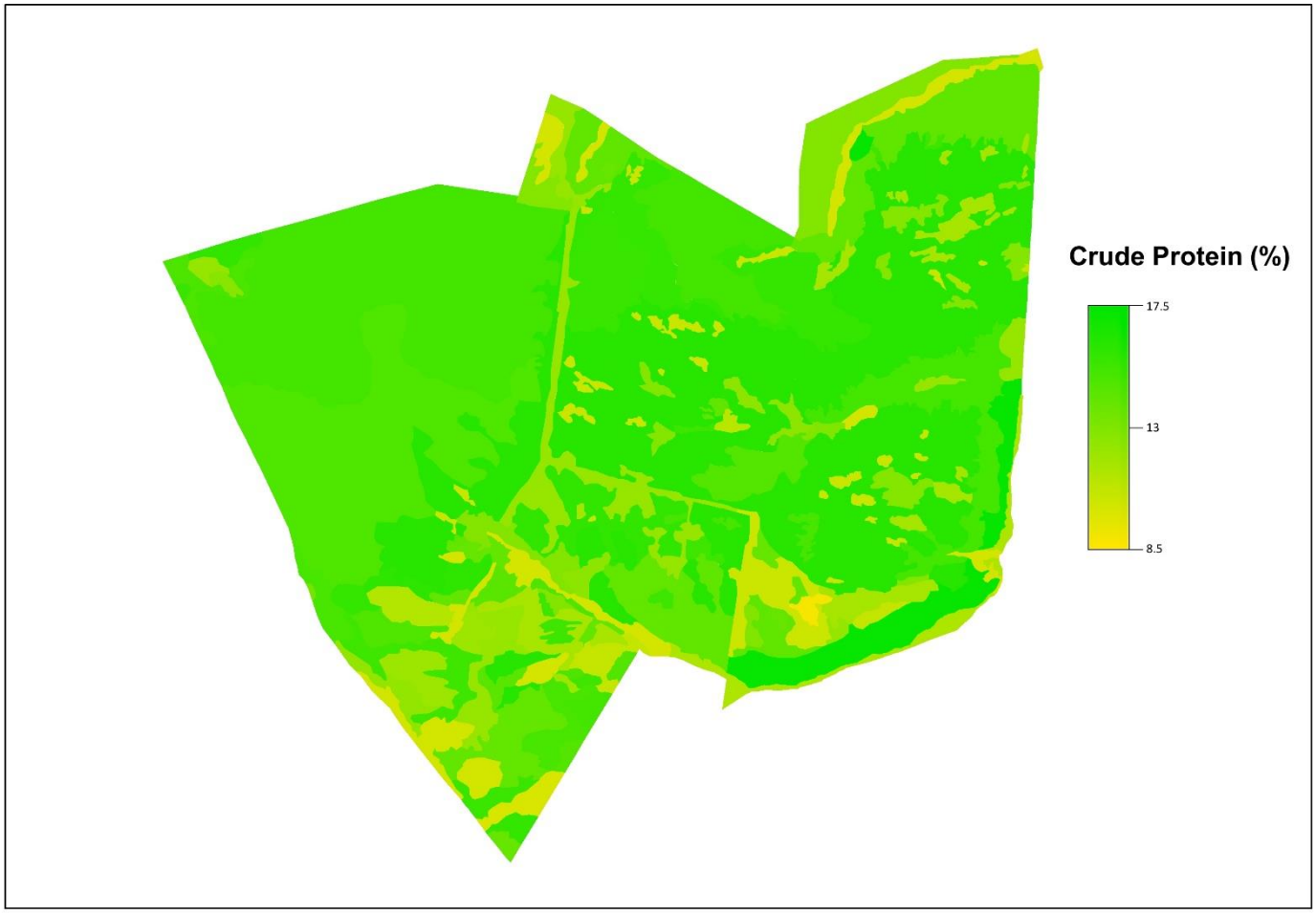


Figure 26: Map to show the estimated digestibility and crude protein availability of different vegetation communities at Squallacombe and Aclands, based on the species composition of the different communities.

3.3 Results

3.3.1 Nutritional quality of upland plants

During autumn sampling, there were interspecies differences in dry matter (Figure 14), neutral detergent fibre (Figure 15) digestibility (Figure 16), metabolisable energy (Figure 17), and crude protein (Figure 18). Values ranged from 26% (*G. saxatile*) to 47.6% (*E. angustifolium*) for dry matter content; from 58.8% (*N. stricta*) to 72% (*A. odoratum*) for digestibility; from 9.2MJ/Kcal (*N. stricta*) to 11.3MJ/Kg (*A. odoratum*) for metabolisable energy; from 38.1% (*C. vulgaris*) to 65.9% (*N. stricta*) for neutral detergent fibre; and from 10% (*D. flexuosa*) to 23.7% (*G. saxatile*) for crude protein. There were small differences in the nutritional quality of *Molinia* between sampling locations, with values ranging from 43.9-44.4% for dry matter content, 61.2-62.4% for digestibility, 9.6-9.8 MJ/Kg for metabolisable energy, 55.9-59.4% for neutral detergent fibre, and 12.4-15.3% for crude protein.

Species also differed in all measures during spring sampling (Figures 14, 15, 16, 17 & 18). Values ranged from 12% (*Sphagnum* spp.) to 43.2% (*E. tetralix*) for dry matter content; from 54.8% (*Sphagnum* spp.) to 70.4% (grassland mosses) for digestibility; from 8.6MJ/Kg (*Sphagnum* spp.) to 11.1MJ/Kg (grassland mosses) for metabolisable energy; from 12.5% (*Sphagnum* spp.) to 65% (*N. stricta*) for neutral detergent fibre; and from 6.9% (*F. ovina*) and 22.8% (*G. saxatile*) for crude protein. Values for *Molinia* sampled from different habitats ranged from 33.6-36.9% for dry matter content, 64.1-65.2% for digestibility, 10.1-10.2MJ/Kg for metabolisable energy, 52-55.1% for neutral detergent fibre, and 15.3-17.8% for crude protein.

Dry matter content of species was significantly higher in autumn than in spring ($t_{18} = 6.31$, $p = 6.02 \times 10^{-6}$). However, there was no difference between seasons in digestibility ($t_{18} = 0.01$, $p = 0.99$), metabolisable energy ($t_{18} = -0.04$, $p = 0.97$), neutral detergent fibre ($t_{18} = -0.72$, $p = 0.48$) or crude protein ($t_{18} = -0.15$, $p = 0.88$).

During autumn sampling, there was no significant difference between plant species of different Ellenberg f values in terms of dry matter content ($F_{4,12} = 1.2$,

p = 0.36), digestibility ($F_{4,12}$ = 1.88, p = 0.18), metabolisable energy ($F_{4,12}$ = 1.74, p = 0.21), crude protein ($F_{4,12}$ = 0.56, p = 0.7) or neutral detergent fibre ($F_{4,12}$ = 2, p = 0.16).

During spring sampling, there was no significant difference between plant species of different Ellenberg f values in terms of dry matter content ($F_{4,15}$ = 2.17, p = 0.12), digestibility ($F_{4,15}$ = 1.67, p = 0.21), metabolisable energy ($F_{4,15}$ = 1.6, p = 0.23), crude protein ($F_{4,15}$ = 1.2, p = 0.35) or neutral detergent fibre ($F_{4,15}$ = 0.87, p = 0.5).

3.3.2 Nutritional quality of upland habitats

Comparison of habitats with the exclusion of bryophytes found no significant difference in dry matter (χ^2_6 = 9, p = 0.17; Figure 21) or crude protein (χ^2_6 = 10.73, p = 0.097; Figure 25), but there were significant differences in digestibility (χ^2_6 = 15.38, p = 0.018; Figure 23), metabolisable energy (χ^2_6 = 15.55, p = 0.016; Figure 24) and neutral detergent fibre (χ^2_6 = 18.9, p = 0.0043; Figure 22).

Comparison of habitats with the inclusion of bryophytes found significant differences in dry matter (χ^2_6 = 13.54, p = 0.0035; Figure 21), but no difference in neutral detergent fibre (χ^2_6 = 10.96, p = 0.09; Figure 22), digestibility (χ^2_6 = 9.47, p = 0.15; Figure 23), metabolisable energy (χ^2_6 = 9.07, p = 0.17; Figure 24) or crude protein (χ^2_6 = 8.61, p = 0.2; Figure 25).

3.4 Discussion

Nutritional quality of upland pastures

Dry matter content was significantly higher in autumn than in spring, as would be expected due to maturation of the sward, but there was no significant difference in digestibility between the spring and autumn samplings. Studies typically report a decline in the digestibility of species on semi-natural pastures from spring to autumn (Grant & Campbell 1978; Hodgson *et al.* 1991), and therefore this result may appear unusual. However, as preceding weather conditions will affect the nutritional value of vegetation (Seligman & Sinclair

1995; Lenart *et al.* 2002), it is possible that this finding may reflect the fact that the two samples were collected in different years; for example, the sward from a favourable autumn could perhaps be of a similar quality to a sward from an unfavourable spring.

In general, the digestibility of species appears to be fairly high, with a number of values comparing favourably to values for *Lolium perrene* in upland pastures (Evans *et al.* 2011). Comparison of the relative rank of the different species in different seasons suggests that there could potentially be major interspecific differences on the effect of maturation on digestibility. For example, *A. odoratum* and *P. erecta* ranked 1st and 2nd for digestibility in autumn, yet were 21st and 18th respectively in the spring. The digestibility of *M. careulea* also showed a relative decline between spring and autumn, ranking higher in spring than in autumn. These results might suggest that it is valuable to maintain species diversity in the swards of semi-natural pastures in order to provide digestible forage species throughout the season. A number of dwarf shrub and herb species, such as *V. myrtillus* and *G. saxatile*, ranked highly in both seasons, which could potentially mean that they help to maintain acceptable levels of digestibility throughout the year. As would be expected, the ranking of species by metabolisable energy produced nearly identical results to those of digestibility.

Also as expected, the ranking of species by percentage of neutral detergent fibre shows a close, inverse correspondence to digestibility. This would suggest that interspecific differences in digestibility can largely be explained by differing levels of neutral detergent fibre. Herb species appeared to offer high levels of protein in both seasons, with *G. saxatile* having the highest levels of crude protein in both autumn and spring. In contrast, graminoids typically contained relatively low levels of crude protein in both seasons.

While numerous factors contribute to the quality of a forage, a combination of high crude protein content and high digestibility should be indicative of high grazing value. Based on this, *G. saxatile*, *P. erecta* and *N. ossifragum* appeared to be relatively good quality forage species on this autumn sampling date, with digestibility >64% and crude protein >18% (Figure 19) comparing favourably

with reported values for *Lolium perrene* (in an upland pasture, mean digestibility 64.25% and mean crude protein 18.93%; from Evans *et al.* 2011). In spring, *G. saxatile* again ranks highly, with *C. vulgaris*, *E. tetralix*, *Agrostis* spp. and turf mosses (Figure 20) also offering similar quality to *Lolium perrene*.

Inclusion of bryophytes, particularly *Sphagnum* spp., in the spring sample produced some unusual results; in particular, the finding that *Sphagnum* spp. had the lowest digestibility, while also having the lowest percentage of neutral detergent fibre is perhaps counterintuitive. However, in common with other bryophytes, the physical structure of *Sphagnum* differs from that of the vascular plants in numerous ways (Weston *et al.* 2014), and it may be that these structural differences have produced some of the extreme values seen for *Sphagnum*. These results appear to suggest that neutral detergent fibre content is not the driving factor behind the low digestibility of *Sphagnum*.

The extreme values of the two bryophyte groups had a significant impact on the quality of the different habitats, with notably different results when they were excluded from the analysis. Due to their disproportionate effect on the sward quality values, it is perhaps more informative to compare values for swards with the exclusion of bryophytes. When only vascular plants are included, there are significant differences in values for digestibility, metabolisable energy and neutral detergent fibre. The result for digestibility appears to be due to the lower values in bracken-dominated and dry grassland habitats. The bracken result may be an artefact of the low species diversity, with a sward almost entirely composed of *H. lanatus* and *A. odoratum*. Vegetation surveys were carried out in spring when these species had relatively low values for digestibility, but maturation varies between species resulting in inter-specific differences in seasonal change of nutritional quality (Grant *et al.* 1978). As *A. odoratum* had the highest digestibility among the autumn samples it is possible that the bracken-dominated habitats would offer higher quality grazing at other times of year. The lower values for drier grassland habitats are likely due to the presence, at varying densities, of the low-quality *N. stricta*.
The same explanation might result in the apparent higher values of neutral detergent fibre in bracken-dominated and dry grassland habitats. Neutral detergent fibre values also appear to be considerably lower in blanket bog

habitats, and this may be due to the lower cover of graminoids in these habitats, and the relatively high cover of dwarf shrubs and herbaceous species.

Habitat mapping suggests that there may be little overlap between areas of high protein content and high digestibility at the Squallacombe and Aclands site (Figure 26). Rush-dominated and valley mire habitats appear to support highly digestible communities but have a low crude protein content, whereas swards in bracken-dominated habitats seem to be protein rich but have relatively low digestibility. Blanket bog, transitional bog, and *Molinia*-dominated habitats appear to offer reasonably high values for both measures. Further work will be required to validate this technique, and mapping of sward quality makes a number of assumptions. Firstly, it is assumed that variation in digestibility and crude protein will be relatively consistent within habitat patches. Secondly, it is assumed that differences between habitats are consistent over time, with the relative value of different habitats remaining the same in different years. It would be valuable to obtain estimates over a number of years to determine temporal variation in habitat quality. Nevertheless, it is presented here as a potential means of visualising the spatial variability in habitat quality at a site, allowing the identification of broad-scale patterns of sward quality.

Overall, aside from a few exceptions the difference between the total sward quality of different habitat types appears to be relatively small. Differences that do exist can potentially be explained by differences in species composition, but it is likely that over the course of a growing season the relative value of different habitats will vary. All habitats are able to offer some grazing value, with those of higher species diversity perhaps able to offer improved feeding opportunities over the course of a year. The findings suggest that the total sward value of improved upland habitats, such as those modified by ploughing and liming, will not necessarily offer an improvement over habitats which have received less manipulation. Results demonstrating increased weight gain of livestock in such habitats (Common *et al.* 1997; Common *et al.* 1998; Critchley *et al.* 2008; Fraser *et al.* 2013) could potentially be due to selective feeding by the animals, and sufficient cover of adequate quality species within such habitats to improve animal performance despite a total sward value similar to rougher pastures.

There are a number of limitations to the approach used here. While the results may provide an indication of the relative quality of a number of different moorland plant species on the sampling day, a more comprehensive sampling effort will be required to validate the results. The taking of multiple samples for each species, from different sites, and in multiple years, would be highly desirable in order to determine how consistent the interspecific differences in quality really are. Nutritional quality of an individual plant can be affected by a number of factors such as, for example, its growing conditions, and therefore the collection of numerous samples from different sites would minimise the possibility of recording anomalous values of quality. The work would also be improved by extending the sampling season to include multiple dates from spring through to autumn, in order to track changes in quality over the course of the growing season, and to properly monitor how the quality of different species changes as they mature. Confidence in the approach to estimating the quality of different habitat types could be improved by taking mixed vegetation samples of known species composition, measuring their nutritional quality, and comparing these to the estimates.

The effect of peatland restoration on sward quality

The findings suggest that peatland restoration might not have a detrimental impact on the grazing value of a sward. There is no clear association between quality and wetness of habitat based on Ellenberg F Values, so an increase in species favouring wetter conditions, as might be expected following rewetting of peat, would not result in a change in quality.

Comparison of the total sward values of the different habitats associated with peatland restoration could suggest a similarly limited impact. At least in the short-term, change following rewetting will be concentrated in areas close to drainage ditches. *Molinia*-dominated communities represent the pre-restoration state, as these are the habitats which dominate following drainage of blanket bog. Transitional bog, and blanket bog communities, represent the hoped for

outcomes of restoration, and providing the water table is raised by rewetting these are the habitats likely to develop (Haapalehto *et al.* 2010; Bellamy *et al.* 2011; D'Astous *et al.* 2013; Menberu *et al.* 2016). As previously noted, *Sphagnum* produced extreme values for a number of measures of nutritional quality, and when included in analyses an increase in *Sphagnum* cover would result in a decrease in overall sward quality due to its low digestibility and protein content. However, *Sphagnum* facilitates colonisation by other mire species (Price & Whitehead 2004), and thick mats of *Sphagnum* are associated with high cover of a diversity of other species. Due to its growth form, it is unlikely that it would comprise more than an incidental component of the diet of grazers, and therefore exclusion from the analyses provides a better indication of the value of the available parts of the sward. When *Sphagnum* is excluded, values for *Molinia*-dominated and bog habitats are very similar in all measures, demonstrating that a change in the prevalence of these habitats might not necessarily result in a significant change in sward quality. Previous studies have questioned whether drainage of peatland was successful in creating favourable grazing (Wilson *et al.* 2011), and this study could potentially support the view that draining peatland does not increase the nutritional quality of a sward. *Molinia*-dominated swards have been shown to produce adequate levels of animal performance (Critchley *et al.* 2008), and the results of this study suggest that they may potentially offer reasonably high grazing value in spring due to their high protein content. However, the persistent quality of certain dwarf shrub and herb species frequent in blanket bog suggest that the habitat may offer adequate grazing for a greater part of the year, which may be particularly important in the autumn. In contrast *Molinia*-dominated habitats appear to offer little grazing value in the autumn due to the lack of species diversity, and the extremely high cover of *Molinia,* which shows a seasonal decline in quality.

An increase in cover of *N. ossifragum*, associated with rewetting, is a legitimate concern for graziers due to the species being implicated in livestock poisonings. However, populations of this species are apparently not always toxic, and the severity of its effects appear to vary regionally, and depending on the grazing animal (Pollock *et al.* 2015). The plant appears to be of high nutritional value, with high digestibility and crude protein content; therefore, if it can be grazed without negative impacts, it could make a valuable contribution to the quality of

a sward. Frequent evidence of grazing on site combined with a lack of reports of livestock poisonings might suggest that at the study locale this species is not particularly toxic.

Overall, there is no reason for peatland restoration to decrease the grazing value of a site, as it is likely to result in a change in the distribution of habitats of similar value. Fresh *Molinia* growth in spring may offer relatively good grazing, but the diversity of bog swards mean that they may provide adequate nutrition for a greater part of the year. It would be worthwhile revisiting this work in future, having allowed more time for vegetation communities to respond to restoration, in order to gain a better understanding of how rewetting might affect agriculture. However, in a typical, extensive upland pasture containing a variety of habitats a change in the proportion of these habitats will have little effect, while the grazing value of other vegetation types should be unaffected.

Conclusion

Agriculture and ecosystem change are closely linked. Humans have a long history of modifying land for agriculture, and a large proportion of the earth's surface has been altered for cultivation or pastoral farming (Asner *et al.* 2004). The productivity of intensive farming systems is relatively consistent due to the fact that nutrient levels and species composition of the sward can be tightly controlled, but in the extensive areas of semi-natural pasture ecosystem change can have a significant impact on productivity. The distribution of different grazing habitats is often dictated by previous attempts at agricultural improvement, with efforts made to alter local hydrology or nutrient input having a major impact on the structure of vegetation communities. However, altering the structure of ecosystems can affect their functionality. As a result, improved agricultural pastures may suffer from problems such as loss of soil stability or soil nutrients, associated with a disruption of ecosystem processes. Furthermore, it appears that the resulting vegetation may not necessarily offer much of an improvement in terms of grazing value.

The increasing interest in restoration ecology is seeing efforts to return large areas of degraded land to their former state. Restoration can conflict with existing land uses such as agriculture due to perceived negative effects on

human activities; however, the restored condition cannot be assumed to be detrimental to current uses. The erosion of ecosystem functionality by land conversion can create landscapes which require high levels of maintenance in order for production to continue. The success of reclamation efforts varies depending on the pre-existing state of the land, with certain habitats more likely to yield success. Reclamation of peatland for agriculture provides an example of a practice which appears to have produced limited results in terms of certain measures of success, such as grazing quality. In such cases where land conversion has been unsuccessful, it may be possible to restore ecosystem function to degraded habitats with no significant impact on existing land use.

Chapter 4: Cattle grazing behaviour in upland pastures

4.1 Background

4.1.1 Ecosystem change and grazing

Large herbivores can play an important role in the functioning of ecosystems. Herbivores are found in a wide variety of habitats worldwide, with their distribution being affected by ecosystem characteristics such as the availability of forage or the physical structure of the environment (Bailey 1996; Joris *et al.* 2009). As a result, herbivores are sensitive to environmental change, and any processes which alter ecosystem structure have the potential to affect the abundance and diversity of herbivores. Globally, trends in populations of wild herbivores are variable. Numerous species have shown population declines due to pressures associated with human activity such as hunting and habitat degradation (Ottichilo *et al.* 2000; Vors & Boyce 2009; Craigie *et al.* 2010). In contrast, some areas currently support unnaturally high densities of herbivores due to human-driven alteration of the landscape and the removal of predatory species (Cote *et al.* 2004; Morellet *et al.* 2007). As well as wild herbivores, livestock are often grazed in natural or semi-natural habitats where they may fulfil a virtually identical role to that of wild species (Veblen *et al.* 2016). Indeed, as a substantial proportion of the land surface is used for pastoral farming, livestock may have an impact on ecosystems by acting as a substitute for wild herbivores where populations are depleted, or adding additional pressure where populations are intact (Asner *et al.* 2004).

Grazing animals can have an influence on ecosystems (Hobbs 1996). As different species of plant respond differently to grazing pressure, herbivores may drive habitat shifts by altering the composition of vegetation communities (Sternberg *et al.* 2000). However, grazers may also limit ecosystem change by maintaining communities of grazing tolerant species and thereby halting the process of succession to a climax community (Milchunas & Lauenroth 1993; Augustine & McNoughton 1998; Adler *et al.* 2001; Diaz *et al.* 2007;). Where populations of herbivores are unsustainably high, overgrazing may occur

resulting in regime shift or complete loss of vegetation cover in sensitive habitats (Sinclair & Fryxell 1985; Li *et al.* 2000). As grazers affect ecosystem structure through their modification of plant communities, they therefore have the potential to alter the functioning of ecosystems (Asner *et al.* 2004). Grazing may destabilise soil through trampling and removal of vegetation cover, resulting in erosion or desertification in extreme cases (Trimble & Mendel 1995). Soil characteristics may be further affected by the addition of nutrients from the excreta of grazing animals (Cao *et al.* 2004; Sharkhuu *et al.* 2016; Wang & Wesche 2016). Furthermore, alteration of vegetation communities may affect abiotic processes, such as the fire regime of an ecosystem (Roques *et al.* 2001; Bowman *et al.* 2011).

Due to the potential for modifying vegetation structure, grazing by wild herbivores or livestock often features as a key component of conservation management programmes. Grazing is frequently used as a tool for maintaining open habitats with high value for biodiversity, for example by promoting floristic diversity and reducing the dominance of unfavourable species in grassland or heathland (Howe 1994; Bokdam & Gleichman 2000; Hayes & Holl 2003). However, grazing can also pose problems for conservation schemes. High densities of grazing animals can cause a loss of grazing-sensitive species, or alter species composition to form communities of lower value to conservation (Fleischner 1994; Gordon *et al.* 2004). In addition, the nutrient input from the excreta of grazing animals may encourage and maintain communities of plants favouring fertile soils at the expense of species requiring nutrient poor conditions (van der Waal *et al.* 2011).

While capable of modifying ecosystems, large herbivores are also responsive to ecosystem change. Rising temperatures, associated with climate change, have the potential to affect the distribution and abundance of grazers, with the effects perhaps most noticeable in cooler regions such as the Arctic tundra. In such areas, the effect of a changing climate on herbivores may be mixed. Negative impacts may occur where reduced ice cover alters migration routes (Sharma *et al.* 2009), or changing temperatures result in a trophic mismatch between herbivores and their forage species with an associated effect on breeding success (Post *et al.* 2008). However, where higher temperatures result in scrub encroachment in to tundra areas, it will benefit species favouring scrub habitats

for grazing (Tape *et al.* 2016). With rising levels of CO_2 and warmer temperatures, productivity of vegetation communities is expected to increase (Parton *et al.* 1995), which could potentially benefit herbivores due to the increased quality and availability of forage. Grazers may also be affected by changes in local hydrology. The presence and distribution of ungulates may be heavily influenced by the availability of water, and therefore where human activity alters water availability this can drive changes in the distribution of grazing animals (Wilmers & Levi 2013; Mckee *et al.* 2015).

Grazing animals may be affected when the biotic structure of an ecosystem is changed. Biological invasions have the potential to negatively affect herbivores, for example when ecosystems are invaded by toxic or unpalatable alien plant species the health of grazers may be negatively affected, or animals may be forced to seek other areas for foraging (Sharp & Whittaker 2003; Kohli *et al.* 2006). In contrast, population explosions of herbivorous species may occur where humans have removed keystone predatory species, and as these are frequently among the first animals to be lost through human activity many populations of grazing animals exist at unnaturally high levels (Fuller & Gill 2000).

4.1.2 Habitat selection by large herbivores

Although level of selectivity is highly variable, wild ungulates typically use different habitats at different times depending on their requirements. The biology of individual species heavily influences their habitat use, with aspects such as migration strategy, vulnerability to predation, and tolerance to low-quality grazing all affecting their habitat selection (Anderson *et al.* 2016). In addition to interspecies variation, there may also be differences in habitat use between different sexes of the same species (Main & Coblentz 1996), with, for example, males travelling more widely and occupying a broader range of habitats (Bliss & Weckerley 2016). There is often temporal variation in habitat use, as animals may need to spend time in different areas to suit different requirements. Habitat heterogeneity allows animals to meet their various needs, for example through the provision of areas of cover for shelter and open areas for foraging (Bjorneraas *et al.* 2010; Heurich *et al.* 2015). Differences in habitat

use may vary over the course of day, with cover being of greater importance for resting up during daylight, and open areas being used more heavily at night for feeding (Bjorneraas *et al.* 2010). The habitat preferences of grazing animals will also change over the course of a year as the resource availability varies (Olsson *et al.* 2011). Seasonality can also influence the distribution of entire populations of migratory species, with animals travelling to areas where weather conditions have produced fresh growth of high-quality forage species (Merkle *et al.* 2016).

In wild ungulates, selection of habitats may be affected by competitive interactions with other grazers. Co-occurring species often exhibit some degree of niche partitioning, for example by selecting different forage species from within the same habitat (Darmon *et al.* 2012; Anderson 2016; Sangiuliano *et al.* 2016), or showing seasonal differences in habitat choice to minimise overlap (van Beest & McLoughlin 2014). This niche partitioning may only occur when suitably high population densities are reached, with species sharing the most favourable habitat type when densities are low enough for resources to not be exhausted (van Beest & McLoughlin 2014). In addition to interspecific competition between wild species, grazers may also be forced to use less favourable habitats in order to avoid competition with livestock (Stewart *et al.* 2002). Similarly, the presence of an alien grazer may exclude native animals from preferred habitats if they are less competitive than the non-native species (Faas & Weckerley 2010). However, while competition between species is common, grazing by co-occurring species can facilitate competitors by providing fresh regrowth of vegetation and thereby increasing the nutritional quality of the available forage (Hobbs *et al.* 1996).

Forage characteristics can influence the distribution of grazing animals. The nutritional quality of vegetation is an important factor; for example, where environmental perturbations such as fire result in the localised occurrence of nutrient rich vegetation regrowth, herbivores will often move to take advantage of the higher quality grazing (Venter *et al.* 2014; Raynor *et al.* 2015; Bliss & Weckerley 2016). Seasonal changes in plant quality and availability are also key drivers behind the seasonal variation in habitat use by grazers (Mancinelli *et al.* 2015), and the presence of a particularly favourable species within a habitat patch may dictate the amount of time animals spend grazing the area

(Fortin *et al.* 2003). Migratory animals are able to track areas of good grazing, while residents may be forced to graze swards of increasingly poor quality as plant maturation occurs over the course of the growing season (Hebblewhite *et al.* 2008). Where human activity alters forage distribution, grazing patterns may also be affected; for example, where deforestation produces open pasture land (Brodie *et al.* 2015) or when highly nutritional crops are planted in agricultural landscapes (Sorensen *et al.* 2015), aggregations of herbivores may occur as the animals exploit the availability of high-quality grazing. As well as quality, the quantity of available forage can be an important factor in some environments, with areas of higher vegetation offering greater biomass for grazing (van Beest *et al.* 2013; Seidel & Boyce 2015). As a result, animals may have to make trade-offs between quantity and quality when selecting habitats for grazing, with areas of lower biomass offering higher quality forage but reduced intake potential when compared with mature vegetation stands (Hebblewhite *et al.* 2008).

Abiotic factors also influence the distribution of grazers within a landscape. For example, cold-adapted herbivores may require areas of standing water, or shaded tree cover to assist with thermoregulation (Street *et al.* 2015; Laforge *et al.* 2016). Where temperature regulation is of importance, it can contribute to fine-scale differences in habitat selection between seasons and over the course of a day (van Beest *et al.* 2012; McCann *et al.* 2016). Species inhabiting colder environments may also be affected by the distribution of snow and ice cover, with frozen water bodies allowing animals to migrate and travel between areas of suitable grazing (Leblond *et al.* 2016). Water availability is of greater importance in areas of lower rainfall, with grazers having limited potential to travel far from permanent water bodies due to their need for drinking water (Bailey *et al.* 1996). Physical characteristics such as topography can also affect the distribution of grazing animals, with some species showing a preference for steep slopes for reasons such as reduced risk of competition and disturbance (Sittler *et al.* 2015).

4.1.3 Grazing behaviour of cattle

Globally, cattle are grazed in a wide variety of natural and semi-natural habitats. As in wild ungulates, cattle grazing heterogeneous pastures will select habitats based on factors such as vegetation quality, topography, and distance from water (Falu *et al.* 2014; Homburger at al. 2015). Level of selectivity may be influenced by the area available for grazing; in larger pastures cattle are able to be more selective when choosing foraging areas, but in smaller patches animals may be forced to graze most of the area in order to obtain enough forage (Henkin *et al.* 2007). This means that when cattle are able to move freely across a landscape they may aggregate in areas with high-quality forage or around water bodies, whereas when confined to smaller, enclosed pastures they will use a wider range of habitats (Probo *et al.* 2014). While inter-specific and intra-specific interactions may have less of an effect on livestock than on wild ungulates, they may still affect the grazing behaviour of cattle. Competitive interactions between cattle and wild herbivores vary between habitats and seasons, but cattle are often able to outcompete wild grazers and may displace them from favourable habitats (Beck & Peek 2005; Torstenson *et al.* 2006). Where wild herbivores share pastures with cattle they may affect their grazing behaviour; both positively, promoting fresh regrowth and thereby increasing forage quality, and negatively, by decreasing the quantity of food available (Hobbs *et al.* 2006). Niche partitioning frequently occurs between cattle and wild ungulates, and therefore the negative impacts of competition with cattle are concentrated on those species which would naturally occupy a similar niche (Stewart *et al.* 2002). Other aspects of cattle behavioural biology may influence their habitat use; for example, although only existing as a risk in certain regions, the presence of predatory species such as wolves may affect the amount of time spent by cattle in certain habitats (Laporte *et al.* 2010). Furthermore, as cattle are social animals their use of particular grazing areas may be based on the presence of relatives and other associates (Howery *et al.* 1998).

Cattle grazing behaviour varies over different time scales. As habitat selection can be affected by heat stress it may vary over the course of a day, with shaded wooded and riparian areas being used more heavily during hotter periods in the afternoon, particularly in warmer months (Zuo & Miller-Goodman 2004). Similarly, wooded habitats may be used for shelter during winter months in

colder climates, with animals spending less time in open grass pastures to reduce heat loss (Rubio *et al.* 2008). In arid areas water availability may be of particular importance during the dry season, resulting in cattle aggregating in riparian habitats during these periods (Roever *et al.* 2015). Forage selection is also temporally variable. Choice of forage may vary over the course of a day, with species selected in the morning differing from those selected later in the day (Rutter 2006). Forage selection varies seasonally, with usage of particular species being greater at certain times of year, reflecting differences in the seasonal availability and quality of different plant species (Willms & Rode 1996). Selection of grazing areas is not necessarily consistent between years, with weather conditions affecting the fine scale distribution of favourable vegetation (Santos *et al.* 2001). The level of selectivity varies based on resource availability; for example, cattle grazing arid areas during the dry season are forced to use a wide variety of habitats in order to obtain adequate quantities of forage (Zengeya *et al.* 2014).

The size of cattle decreases their ability for fine-scale forage selection when compared with smaller herbivores such as sheep (Hodgson *et al.* 1991). Where there is a large quantity of easily accessible, high-quality forage, cattle may show greater selectivity than sheep and goats, which are more generalist browsers (Samuels *et al.* 2014). Cattle typically graze areas with a high availability of forage before moving to harder to access patches; for example, in grassland/shrub mosaics, cattle preferentially graze open areas before moving to feed on vegetation growing underneath shrub canopies (France *et al.* 2008). The limited ability for selection means that in rough grasslands cattle may consume high volumes of coarse, low-quality plants when attempting to graze favourable species, unlike sheep which are able to select preferred species from among the taller vegetation (Critchley *et al.* 2008). This can also mean that cattle are less able to maintain diets of high digestibility on low-quality swards, as the proportion of digestible species consumed will be limited by their frequency within the sward (Hodgson *et al.* 1991).

Cattle appear better able to graze woody species than other livestock, and where mixed grazing occurs cattle may use woodland and scrub habitats more frequently than other species (Menard *et al.* 2002; Lamoot *et al.* 2005). Consequently, cattle can show high flexibility in their diet, with a wide range of

species and habitats able to be grazed (Radloff *et al.* 2013). However, although woody plants can be utilised, cattle generally show a preference for graminoids where available, particularly nutrient-rich fresh growth (Lamoot *et al.* 2005), and cattle grazing within forest habitats may select graminoids to feed on (Kingery *et al.* 1996). As a result, fertile, productive grasslands are grazed initially, with a switch to less favourable habitats only occurring where food availability is limited (Putfarken *et al.* 2008). The preference for nutrient rich growth may also affect grazing distribution within a grassland patch, with particularly fertile areas, such as those around lakes and rivers, receiving greater use (Smith *et al.* 1993; Santos *et al.* 2001). Disturbance events, such as fire in grassland, may also encourage cattle grazing as animals take advantage of the fresh regrowth which follows (Clark *et al.* 2014). Indeed, the rapid development of fertile swards following fire can result in cattle abandoning grazing in previously favoured areas, such as those alongside water bodies (Clark *et al.* 2016). Availability of woody or scrub-dominated habitats may be of greater importance in autumn and winter when grasslands produce poor quality, low biomass swards (Menard *et al.* 2002). The influence of nutritional quality on habitat selection appears to be variable, and while factors such as succulence, crude protein content and digestibility may be associated with higher levels of cattle usage, quantity of available biomass may be of equal or greater importance (Wallis *et al.* 1994; Kohl *et al.* 2012; Kaufmann *et al.* 2013). Other requirements, such as distance to drinking water, can also influence habitat selection more heavily than factors relating to quality (Putfarken *et al.* 2008).

Habitat and forage choice can vary between different breeds of cattle, with some actively choosing to graze on woody species within forest habitat even where fertile grassland is available (Bartolome *et al.* 2011). When grazed together, hardy breeds are often able to use a wide variety of species from within the specific habitat for which they have been bred to graze, whereas modern, high productivity breeds are more likely to graze a variety of habitats in order to locate adequate quantities of favourable forage species (Bele *et al.* 2015).

4.1.4 Grazing in upland pastures

As cattle have a limited ability to select from within swards, their diet typically features a relatively high proportion of dead material and low-quality species when grazing upland pastures (Grant *et al.* 1987; Hodgson *et al.* 1991). In addition, as cattle require relatively long swards in order to obtain suitable volumes of forage, large, robust graminoids such as *Molinia*, *Nardus* and *Juncus* tend to feature more prominently in cattle diet than in sheep (Critchley *et al.* 2008; Holland *et al.* 2008; Fraser *et al.* 2011). The limited ability to select restricts the potential for cattle to graze dwarf-shrub dominated habitats as they may struggle to obtain suitable quantities of forage of high enough a quality (Grant *et al.* 1987). However, cattle can graze blanket bog communities, selecting graminoids such as *Molinia*, *Trichophorum* and *Carex*, and avoiding woody dwarf-shrubs except during periods of low food availability (Grant *et al.* 1987). The avoidance of dwarf-shrubs means that cattle grazing can be compatible with heather regeneration in grassland-heather mosaics, as cattle will actively select graminoids rather than browsing heather (Mitchell *et al.* 2008; Critchley *et al.* 2013).

While cattle are frequently grazed on hill pastures, sheep grazing is far more common in uplands. Cattle may struggle to maintain suitable levels of performance on upland pastures during unproductive times of year, or when restricted to certain low-quality sward types (Common *et al.* 1994). In sheep grazing a typical blend of upland habitats, acid grassland appears to be most heavily selected, with blanket bog used least frequently (Williams *et al.* 2010; Williams *et al.* 2012). Like cattle, sheep select graminoids preferentially (Grant *et al.* 1987), and improvement methods such as peatland drainage appear to be relatively ineffective in terms of increasing grazing value unless they are able to produce graminoid-rich swards (Wilson *et al.* 2011). Indeed, the size and distribution of dense, grass-dominated swards appears to be a good predictor of sheep usage of an area within an upland pasture (Williams *et al.* 2009).

In sheep, graminoids make up the majority of the diet, , but dwarf-shrubs also feature frequently, possibly because their fine-scale forage selection allows them to consume the relatively nutritious fresh growth from among the woodier material (Fraser *et al.* 2009). As with cattle, sheep may graze dwarf-shrubs more frequently in autumn and winter when maturation has reduced the quality

of grassland habitats (Welch 1998; Fraser *et al.* 2009), with blanket bog and heather moorland used more frequently at these times of year (Williams *et al.* 2010). Where there is high usage of dwarf-shrubs sheep can prevent regeneration of grazing-intolerant species such as heather, with patches of heathland close to grassland being particularly heavily affected (Oom *et al.* 2008). The spatial distribution of grass lawns affects usage of other habitats; dwarf-shrubs are browsed more heavily where grassland occurs in small patches among heath communities, while large, continuous patches of grassland reduce grazing on surrounding dwarf-shrubs (Clarke *et al.* 1995). Nevertheless, fine-scale habitat heterogeneity may promote the persistence of dwarf-shrubs in grass/heather mosaics, as grazing effects are spread evenly over a wide area (Oom *et al.* 2010).

However, sheep may benefit other vegetation communities, with grazing helping to maintain cover and diversity of blanket bog species on the periphery of mires (Smith *et al.* 2003). In grassland, sheep can increase the cover of coarse, unpalatable grasses such as *Nardus*, as animals will typically ignore such species to select more favourable species from the sward, allowing them to spread through lack of grazing pressure (Hulme *et al.* 1999; Holland *et al.* 2008). Goats are similarly well adapted to grazing infertile upland pastures, and may use a higher proportion of low-quality coarse and woody species, such as *Juncus* and heather, when compared to sheep (Grant *et al.* 1984).

Habitat selection in uplands may be affected by other factors aside from vegetation characteristics. In sheep, the presence of other herbivores such as red deer may influence their choice of habitat (Cuartas *et al.* 2000), although the effects of competition appear to vary regionally (Hester *et al.* 1999). Topography may also affect the distribution of animals on a site, and the extent of their use of particular areas. Sheep generally prefer to graze in flatter, gently sloping areas where possible (Sheath 1983). However, preferences may be altered when food supply is limited; in winter, sheep do not show a preference between steep and flatter areas when grazing due to the overall difficulty in obtaining an adequate intake of forage (Lopez *et al.* 2003). As in sheep, cattle usage of an area is negatively associated with the level of slope, with animals preferring to graze flatter ground (Kaufmann *et al.* 2013). Sheep appear to be resilient to the harsh environmental conditions of hill pastures, and availability of shelter

appears to play little role in dictating selection of grazing patches (Duncan *et al.* 2001).

4.1.5 Hypotheses

This chapter focuses on two questions:

1. Which upland habitat types are used most heavily by livestock?

2. Will peatland restoration affect the grazing behaviour of livestock?

In order to compare levels of cattle use of different habitat types, dung counts were carried out at thirty randomly located points within each habitat category to provide an estimate of cattle activity within each habitat. These were supported further by the use of timelapse cameras, which were set at points around the site overlooking different habitats and left to film, so that cattle activity could be recorded in different areas. These results were used to compare levels of usage of pre- and post-restoration habitats, but in order to study this further dung counts were carried out in a different year at randomly located plots within the main restoration.

It is hypothesised that livestock activity will not be distributed evenly between habitats, and that peatland restoration might have a negative impact on livestock grazing due to the expected increase in cover of less favourable dwarf-shrub species.

4.2 Materials and methods

The study was carried out at the Squallacombe and Aclands site (description in Chapter 2.2.1), which was selected for its representative range of Exmoor's common moorland habitats, and the presence of a grazing herd of ~40 Red Devon cattle from midsummer to early autumn (June – October) each year. Small numbers of sheep are also present intermittently, while herds of wild red deer are present intermittently all year round.

4.2.1 Dung density surveys

The study area differed between field seasons. In 2014-15, data collection was carried out to determine the effect of peatland restoration on cattle grazing. As a result, work focused on the main catchment area of Aclands, encompassing the habitats which are likely to be most heavily affected by rewetting. In the 2015-16 field season, the focus changed to compare levels of grazing in different upland vegetation communities. As a result, the study area was expanded to the outer perimeter of the site, meaning that the Squallacombe restoration site and areas of improved pasture were included. This work was carried out in order to identify the habitats and areas of particular value for grazing.

2014 cattle dung survey

Stratified random sampling was used to survey cattle usage of the restoration area at Aclands. Based on ordnance survey grid references, the study area was divided in to 57 100 m^2 plots, and three points were randomly generated within each of these squares giving a total of 171 points. If there was overlap between any two points then one was deleted and a replacement generated.

The number of cattle dung piles per 100 m^2 was used as to estimate cattle use of a plot, as this is a reliable indication of time spent in an area (White *et al.* 2001). Surveys were carried out in July 2014, and repeated in October after cattle had been taken off the site. Grid references were entered in to a handheld GPS device, and each point was visited in order to record cattle dung density with location accuracy to 2m. The number of dung piles was counted in a 100 m^2 circle (measured radius of 5.64 m) surrounding each grid reference point. In July, while cattle were active on site, all 171 counts were carried out within three days of each other in each sampling season to minimise the potential for increased grazing time to result in higher dung densities. Cattle were not observed in the sampling area during data collection, and therefore it is unlikely that the difference of three days between surveys will have had a major effect on results.

2016 cattle dung survey

Stratified random sampling was again used for the 2015/16 field season. However, this time sampling points were separated by habitat, based on previously created habitat maps of the site (Chapter 2.2.2). Thirty survey points were randomly generated in ARCmap, in each of seven broad habitat

categories: bracken-dominated, dry grassland, rush-dominated, valley mire, *Molinia*-dominated, transitional bog, and blanket bog (see Chapter 2.2.2 for habitat descriptions), giving a total of 210 points. A buffer was set at habitat boundaries to ensure that the generated points did not overlap different habitat types. Habitats identified by mapping proved to be accurate in every case except for one; as a result, the final count included 31 survey points in dry grassland and 29 in transitional bog. The habitat map was subsequently corrected to reflect the actual habitat boundary between the two patches.

Survey work was carried out on three survey dates from January-March 2016 while cattle were absent from the site. Cattle dung density was recorded at each randomly generated point using the same method as the 2014 surveys.

4.2.2 Timelapse survey

Two Brinno TLC200 timelapse cameras were used to determine levels of usage of various habitats. Cameras were placed in weatherproof cases and fixed in to their selected positions with elastic grappling hooks. The camera lens has a viewing angle of 59°. Both cameras were set up to capture images every 30 seconds during daylight hours. Thirty seconds was chosen as it was deemed a sufficiently short interval to capture any cattle activity, while being infrequent enough to conserve battery life and memory card storage; under these conditions the cameras could be left for periods of at least one month. The cameras produced an output of an avi video for each day of filming. Each video was studied after the field season had ended in order to determine whether cattle visited the recorded location on each day. Analysis of the footage suggested that cattle were discernible at up to at least 500 m. Footage was further analysed in order to identify instances of grazing. Grazing behaviour could be identified when cattle remained in one area for long periods, moving short distances between frames and following indeterminate paths, which frequently doubled back on themselves. When animals were close enough to the camera lens it was possible to see that their heads were down grazing, in addition to the aforementioned movement behaviour. In contrast, animals in transit would rapidly pass through, often in lines rather than in a spread out herd, with heads raised.

Timelapse surveys were carried out in the autumn of 2015. The two cameras were placed at various points around the site (minimum two days, maximum 15) in order to provide coverage of a wide variety of habitats and locations. The length of time a camera was left in place was largely determined by weather, as locations were not changed during days of heavy rainfall due to the potential risk of water entering the camera as batteries or memory cards were replaced. Cameras covering large areas containing a variety of habitats were typically left in place for between seven and 14 days, while those with more restricted views were moved more frequently. The aim of this work was to determine which parts of the site cattle were spending the most time in. Cameras were left out between 9th September and 10th November 2015. One camera had technical problems during the field season, which meant that the battery died unusually quickly, resulting in a total of 25 missed filming days spread over three separate locations. The other camera had no issues during filming. A map of camera locations is provided in Figure 27, and examples of screenshots from each camera location are provided in Figures 28 and 29.

4.2.3 Statistical analysis

For the 2014 data, points were assigned to habitat categories based on previously created habitat maps (Chapter 2.2.2). Chi-squared analysis was carried out to determine whether counts of cattle dung in different habitats were as expected based on the number of sampling points within that habitat (testing the null hypothesis that distribution of cattle dung was independent of the distribution of different habitats). Analyses were carried out on the results for both spring and autumn to determine whether there were any seasonal differences in cattle use of different habitats.

For the 2016 data, a Kruskal-Wallis one-way analysis of variance was carried out to determine whether the density of cattle dung differed between the seven broad habitat categories.

In addition, a Kruskal-Wallis one-way analysis of variance was carried out to determine whether dung density differed between pre- and post-restoration habitats. This analysis used the results of the 2016 survey, with the pre-

restoration category including the *Molinia*-dominated habitats and the post-restoration category including transitional bog and blanket bog habitats.

For the timelapse survey, camera footage was reviewed and the number of days of cattle presence noted for each location. Chi-squared analysis was then carried out to determine whether the number of cattle visits for each camera location differed from what would be expected based on the length of time the camera was left at the location (testing the null hypothesis that the number of recorded cattle visits to a habitat was independent of the amount of time a camera was left in that habitat). Chi-squared analysis was also carried out to determine whether the number of days on which cattle were recorded grazing differed from what would be expected based on the length of time the camera was left at the location (testing the null hypothesis that the number of days on which grazing was recorded was independent of the amount of time a camera was left in that location.

3.2.4 Mapping livestock habitat use

Values for dung density from the 2016 field season were used to produce a heat map of cattle grazing activity on the site based on the distribution of broad-scale habitat categories. These were based on the previously created habitat maps (Chapter 2.2.2). An average value for dung density was calculated for each different habitat category, and then used to create a site map showing the expected spatial variability in dung density based on the presence of particular habitats.

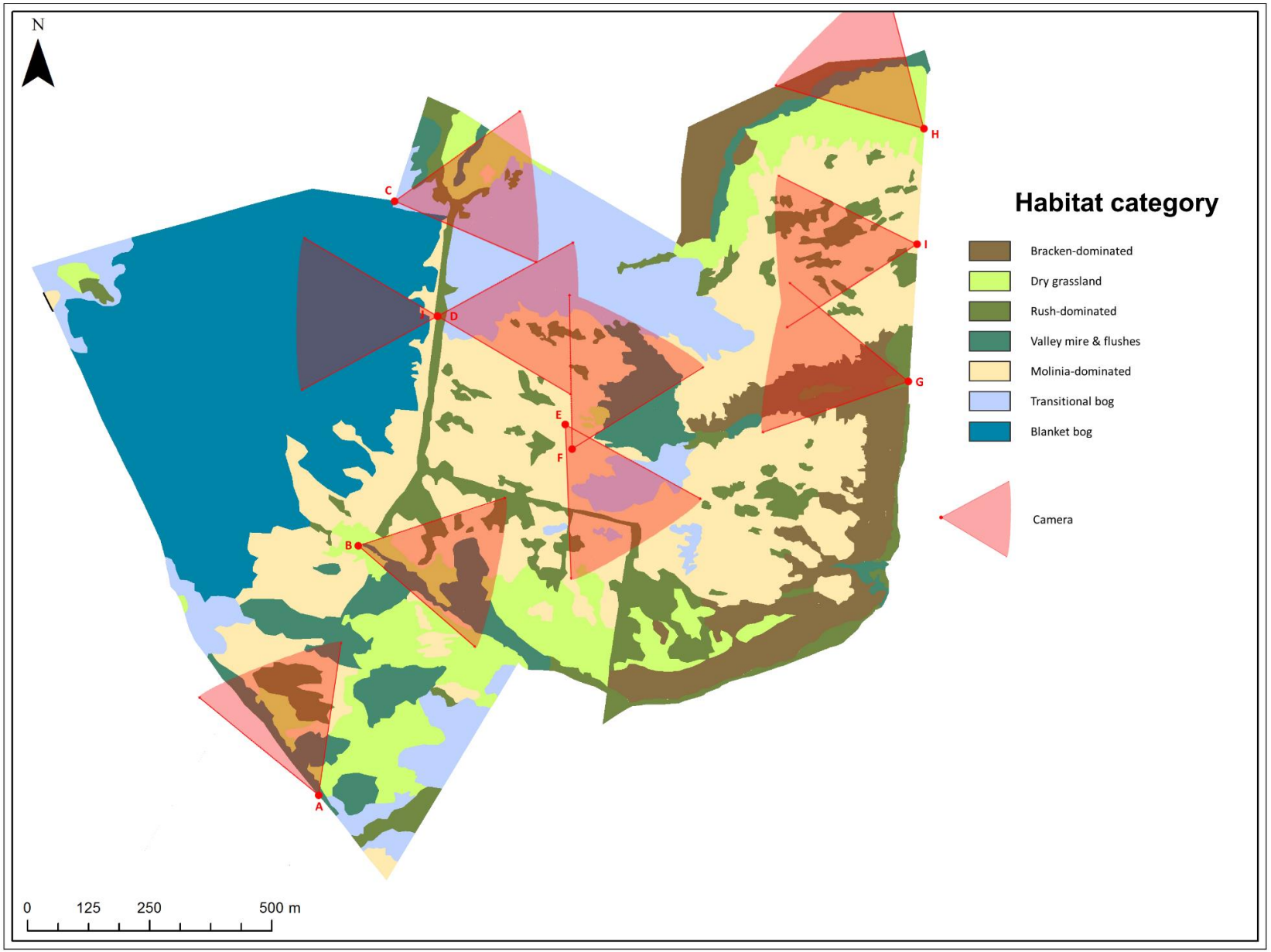


Figure 27: Map showing the positions, approximate viewing areas, and habitats covered by the cameras used during the timelapse camera survey.

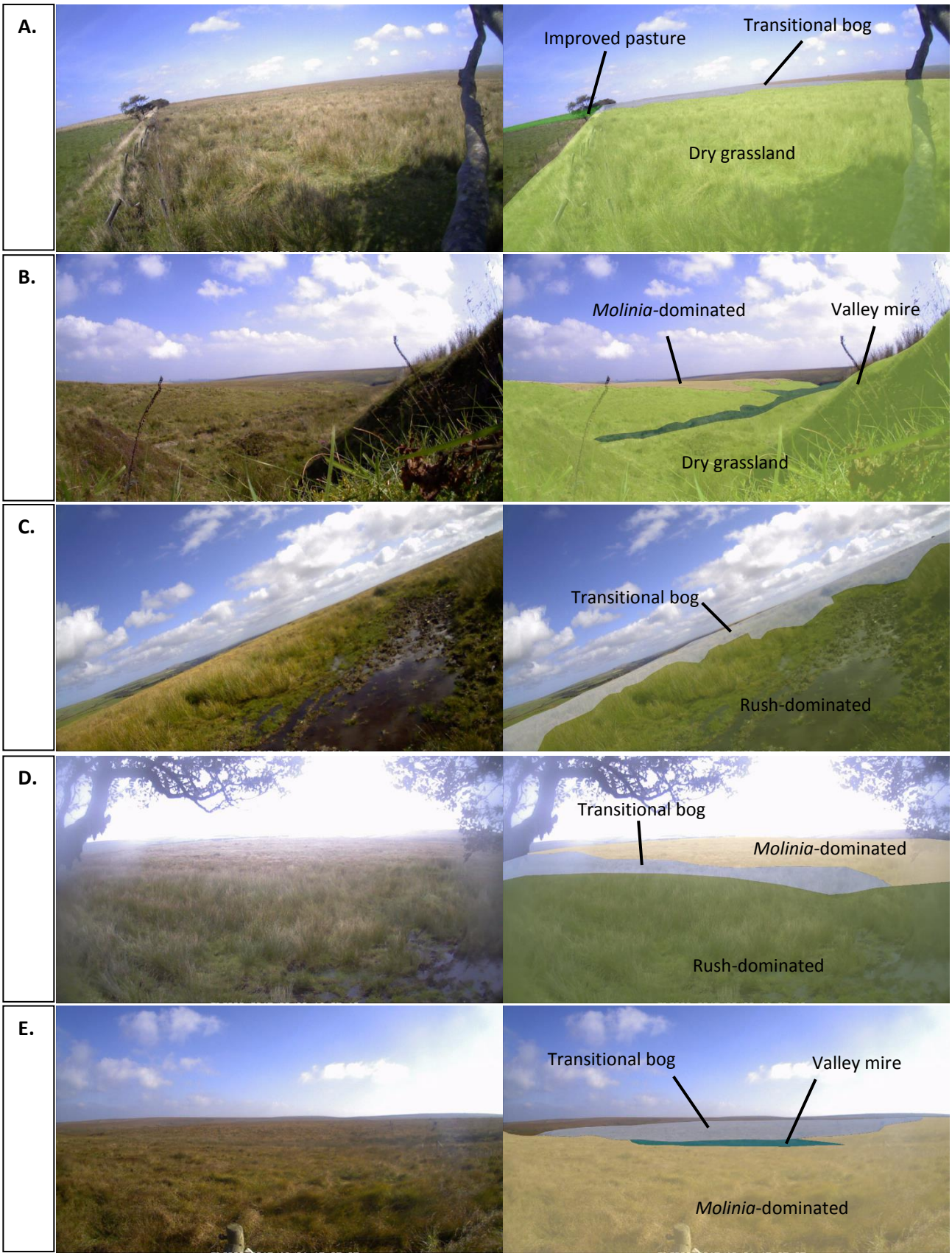


Figure 28: screenshots of the view covered by cameras in positions A-E (left column), and an estimate of different habitat types visible in the images (right column). Letters correspond to locations shown in figure 27.

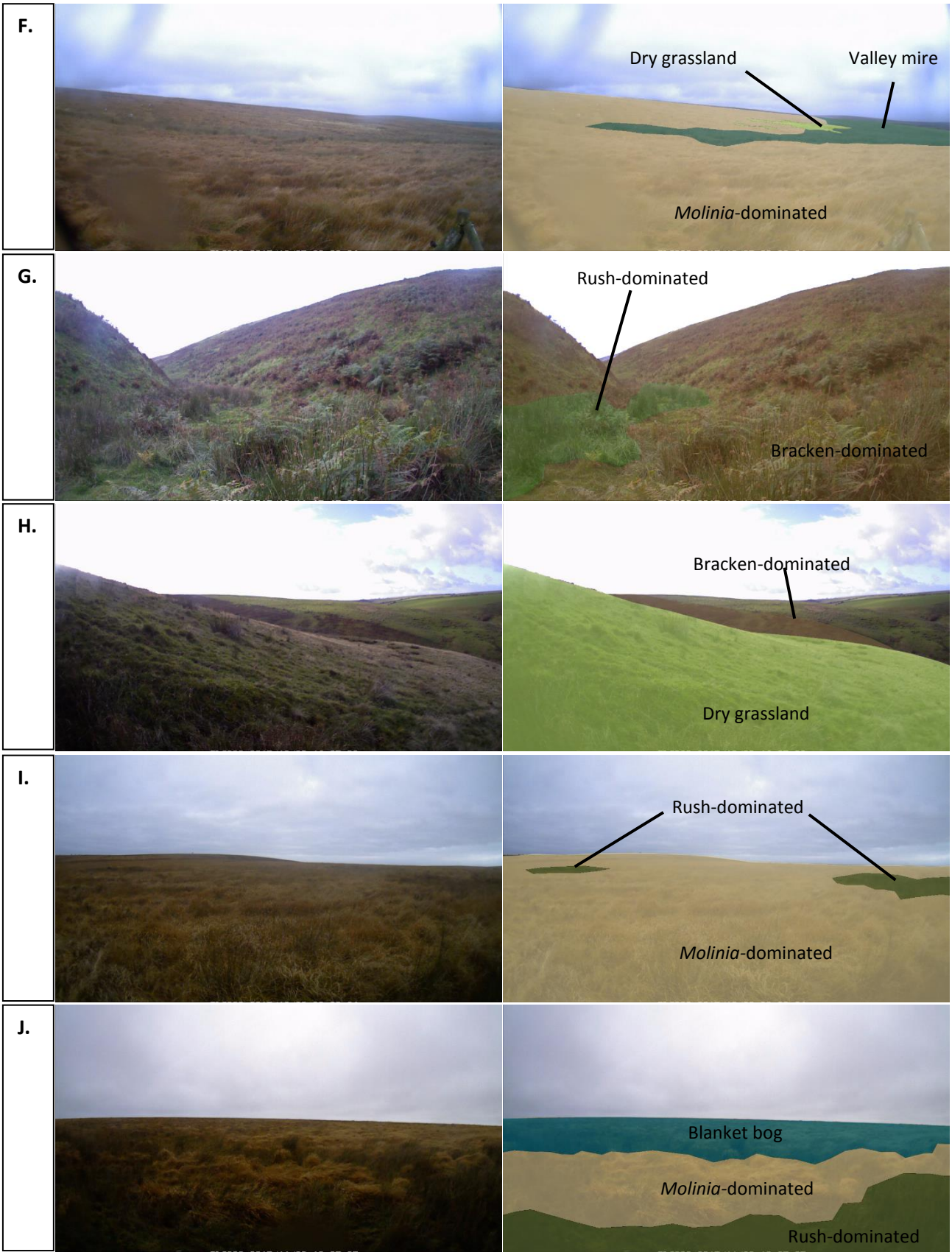


Figure 29: screenshots of the view covered by cameras in positions F-J (left column), and an estimate of different habitat types visible in the images (right column). Letters correspond to locations shown in figure 27.

Table 10: Vegetation communities recording high (≥3 per 100m^2) densities of cattle dung during surveys in the summer and autumn of 2014. Habitat categories are as follows: BO = blanket bog; BR = bracken-dominated; GS = dry grassland; MO = *Molinia*-dominated; RD = rush-dominated; TR = transitional bog. Community descriptions are given in Chapter 2.2.2.

Habitat	Vegetation Community	Dung Count				
		3-5	6-10	11-15	16-20	20+
	Summer					
GS	7 – acidic grassland	1				
TR	19/12 – wet *Molinia*/rush-dominated flush	1				
	Autumn					
BR	1/2 – dense bracken/bracken & dry grass		1			
GS	7 – acidic grassland		1	1		
GS	7/10 – acidic grassland/dense dry rush	1	1			
RD	10 – dense dry rush		4			
RD	11/10 – rush & grassland/dense dry rush				1	
MO	16 – dense *Molinia*	4				
MO	18/10 – dry *Molinia*/dense dry rush	1				
TR	19/21 – wet *Molinia*/recovering mire	1				
TR	20/21 – wet *Molinia* & mire/recovering mire	1				
BO	22/23 – mire hollow/mire hummock	1				

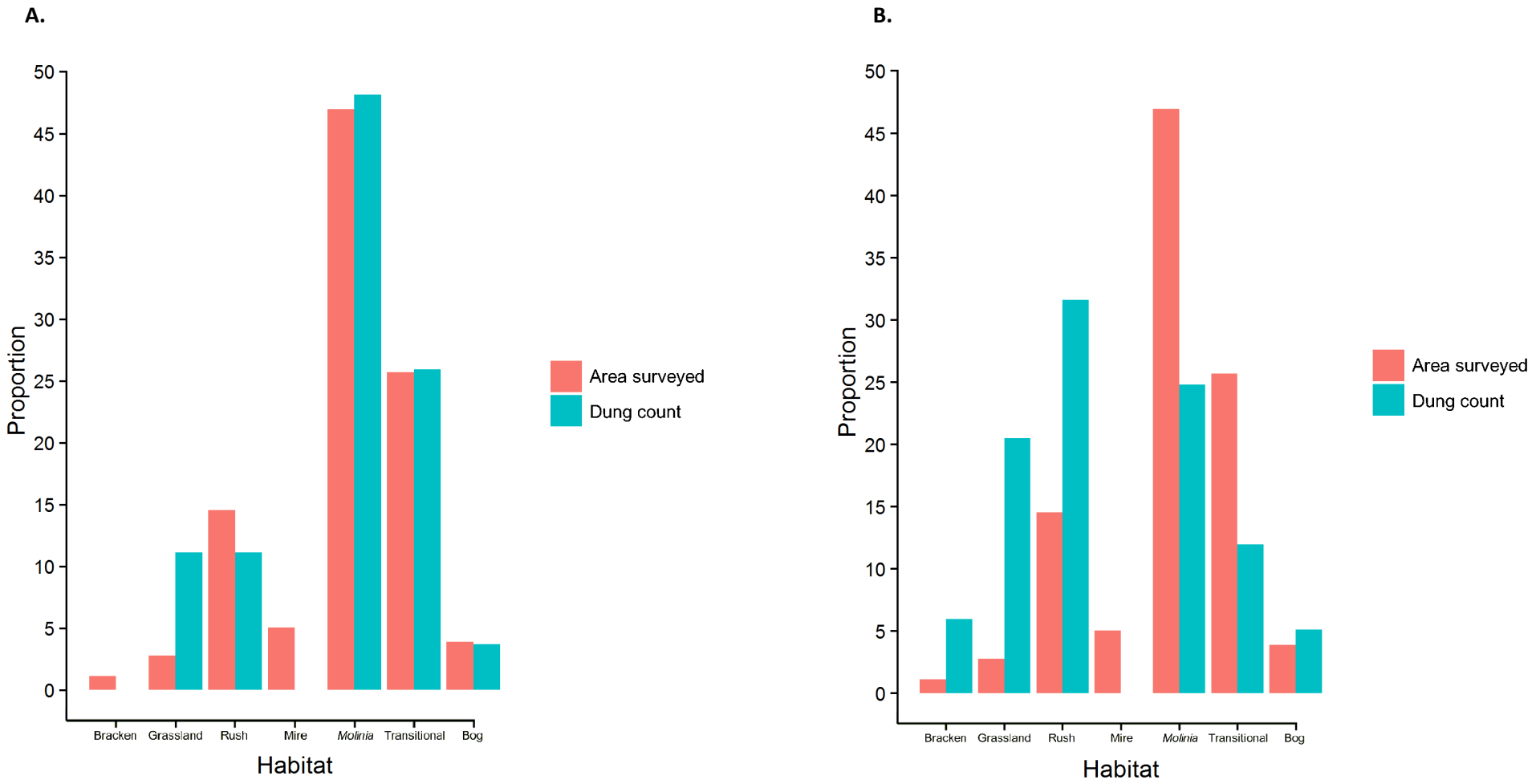


Figure 30: A comparison of the proportion of total area surveyed with the proportion of cattle dung counted in each habitat category for (**A**) summer and (**B**) autumn surveys.

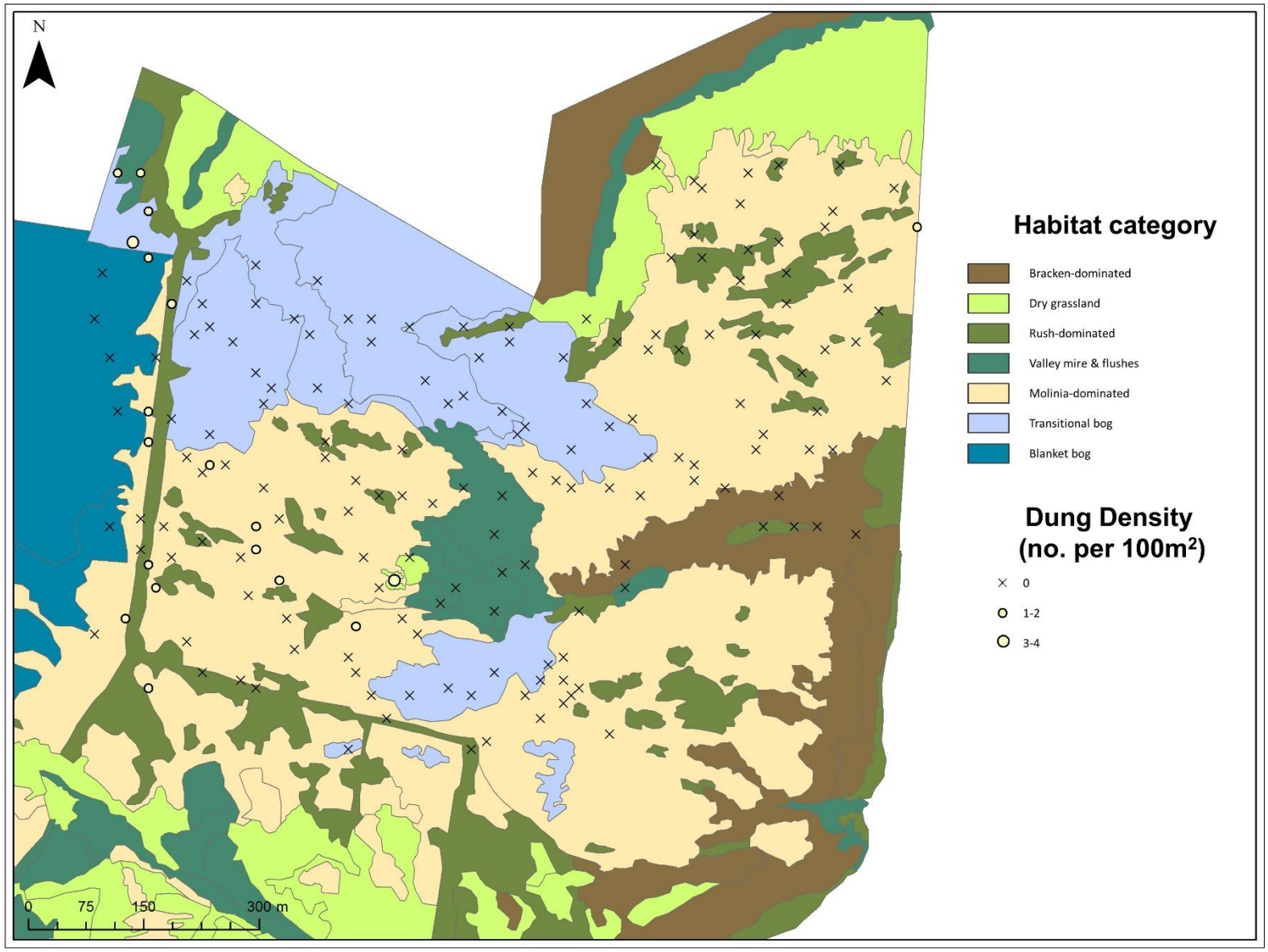


Figure 31: Map showing the density of cattle dung at each sampling point in July 2014.

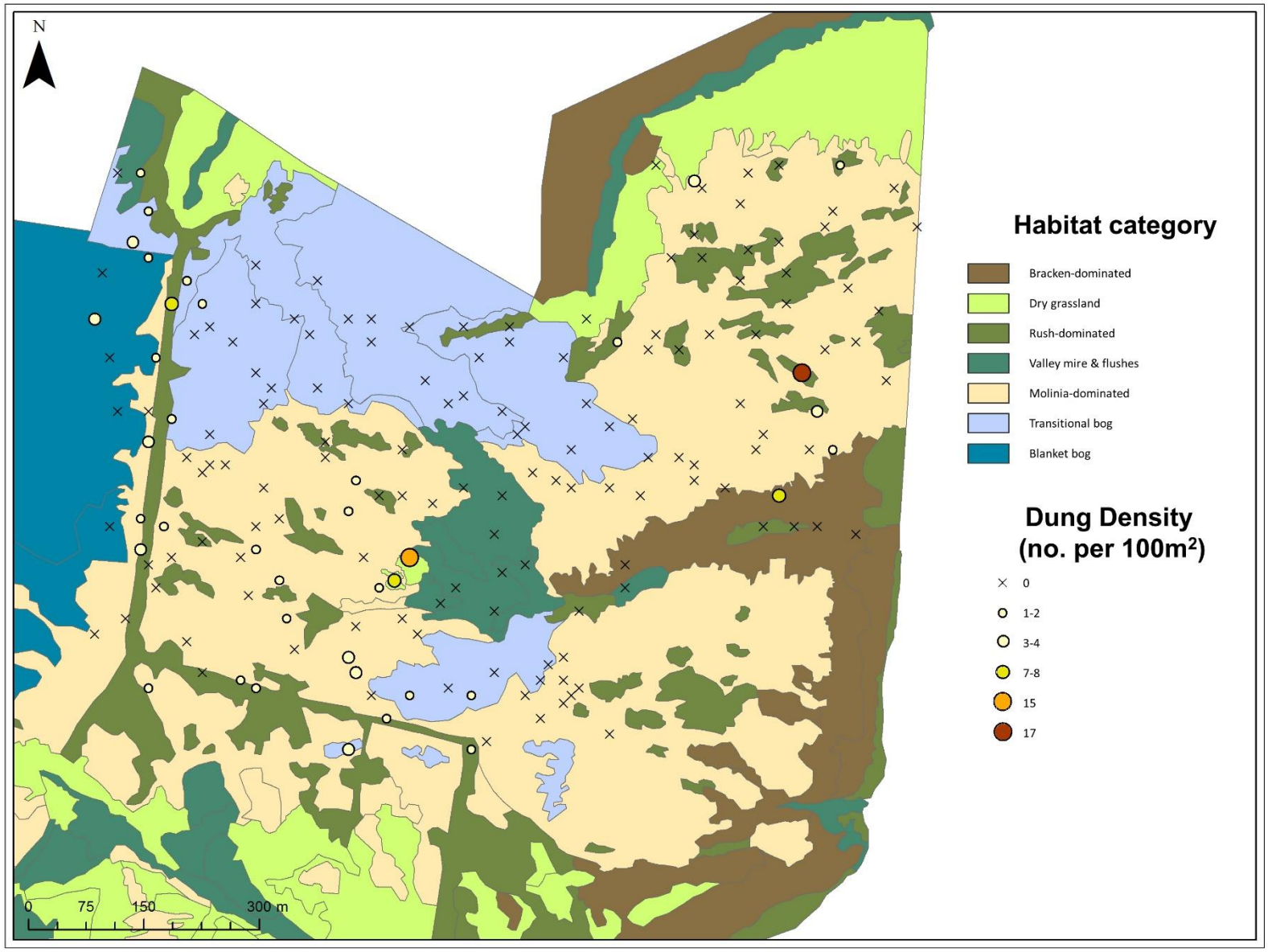


Figure 32: Map showing the density of cattle dung at each sampling point in October 2014.

Table 11: Vegetation communities recording high (≥3 per 100m^2) densities of cattle dung during surveys in 2015/16. Habitat categories are as follows: BR = bracken-dominated; GS = dry grassland; RD = rush-dominated; VM = valley mire. Community descriptions are given in Chapter 2.2.2.

Habitat	Vegetation Community	Dung Count				
		3-5	6-10	11-15	16-20	20+
BR	1/2 – dense bracken/bracken & dry grass	6				
BR	2 – bracken & dry grass	3	4			1
GS	4 – rough *Deschampsia* grassland	1				
GS	5 – rough grassland		1			
GS	6 – minerotrophic grassland	1	4	4	1	
GS	6/10 – minerotrophic grassland/dense dry rush		1			
GS	7 – acidic grassland	1	2			
GS	7/10 – acidic grassland/dense dry rush	6	3			
RD	9/6 – dense damp rush/minerotrophic grassland		1		1	
RD	10/1 – dense dry rush/dense bracken	2			1	
VM	12 – rush-dominated flush	1				

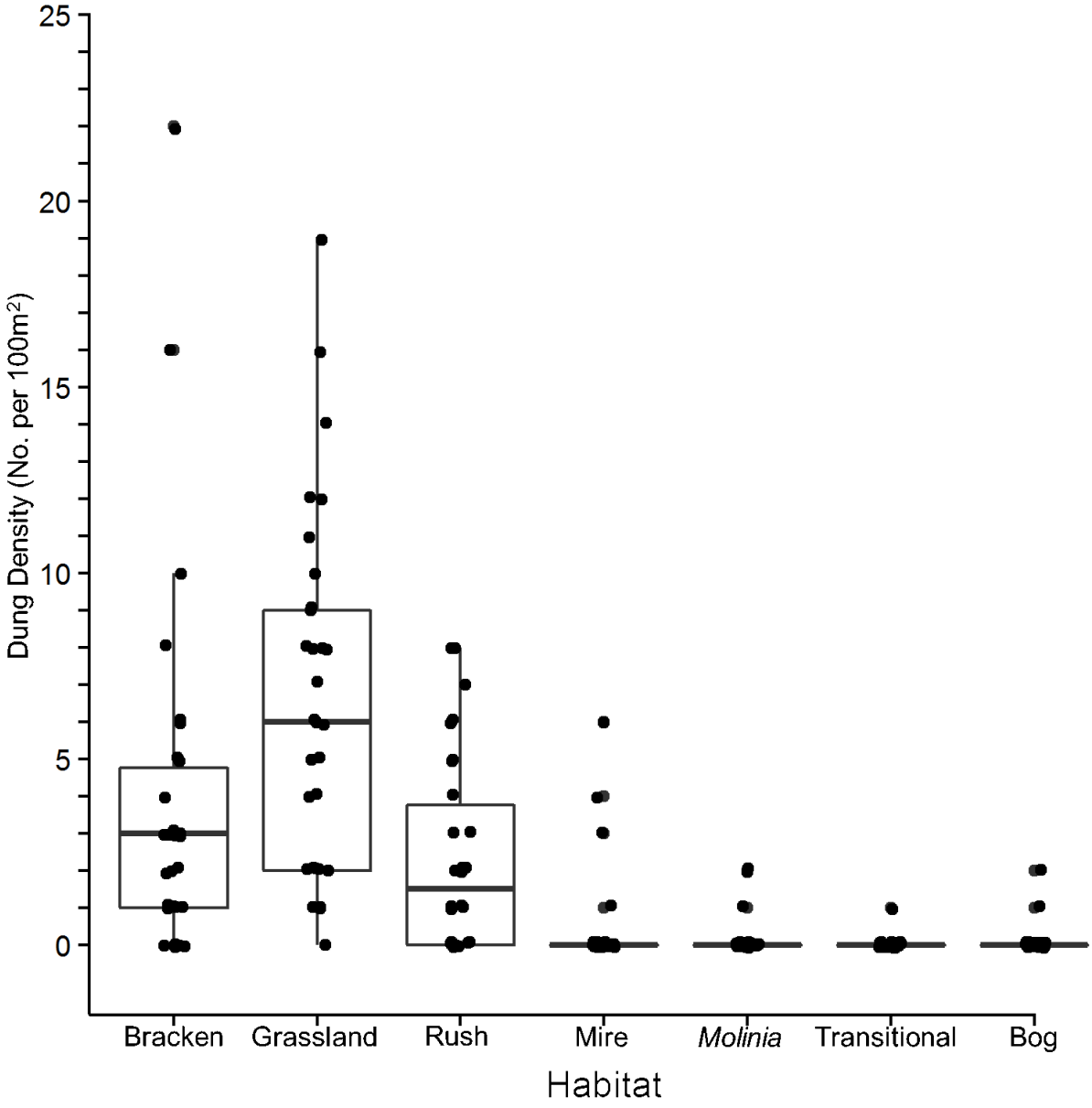


Figure 33: A comparison of the cattle dung density in different habitats recorded between January-March 2016. Points represent dung densities from each individual 100m^2 plot. The centre line of the boxes marks the mean, while the whiskers mark the range, excluding outliers.

Table 12: Number of recorded cattle visits and number of grazing observations from different timelapse camera positions. Letters correspond to the locations shown in Figure 27.

Position	Habitat	Days recorded	Days cattle present	Days cattle grazing
A	Predominantly rush and improved *Agrostis/Festuca* grassland. An improved *Lolium/Trifolium* pasture, outside of the site boundary but accessible to cattle, also visible	15	9	9
B	Mainly dry acidic grassland slopes. Some mire visible in the valley bottoms, and *Molinia* pasture on the plateaus	15	10	10
C	Transitional bog and dense *Molinia*	4	3	0
D	Dense *Molinia*	2	0	0
E	Mainly dense *Molinia*, with valley mire and transitional bog	11	2	1
F	Dense *Molinia* and valley mire. 2 small patches of dry *Agrostis/Festuca* grassland visible	11	1	1
G	Slopes covered in dense bracken, with small patches of dry acidic grassland	12	3	3
H	Dry acidic grassland with bracken slopes visible	13	7	7
I	Dense *Molinia* with patches of rush and transitional bog	6	0	0
J	Blanket bog and *Molinia*	8	0	0

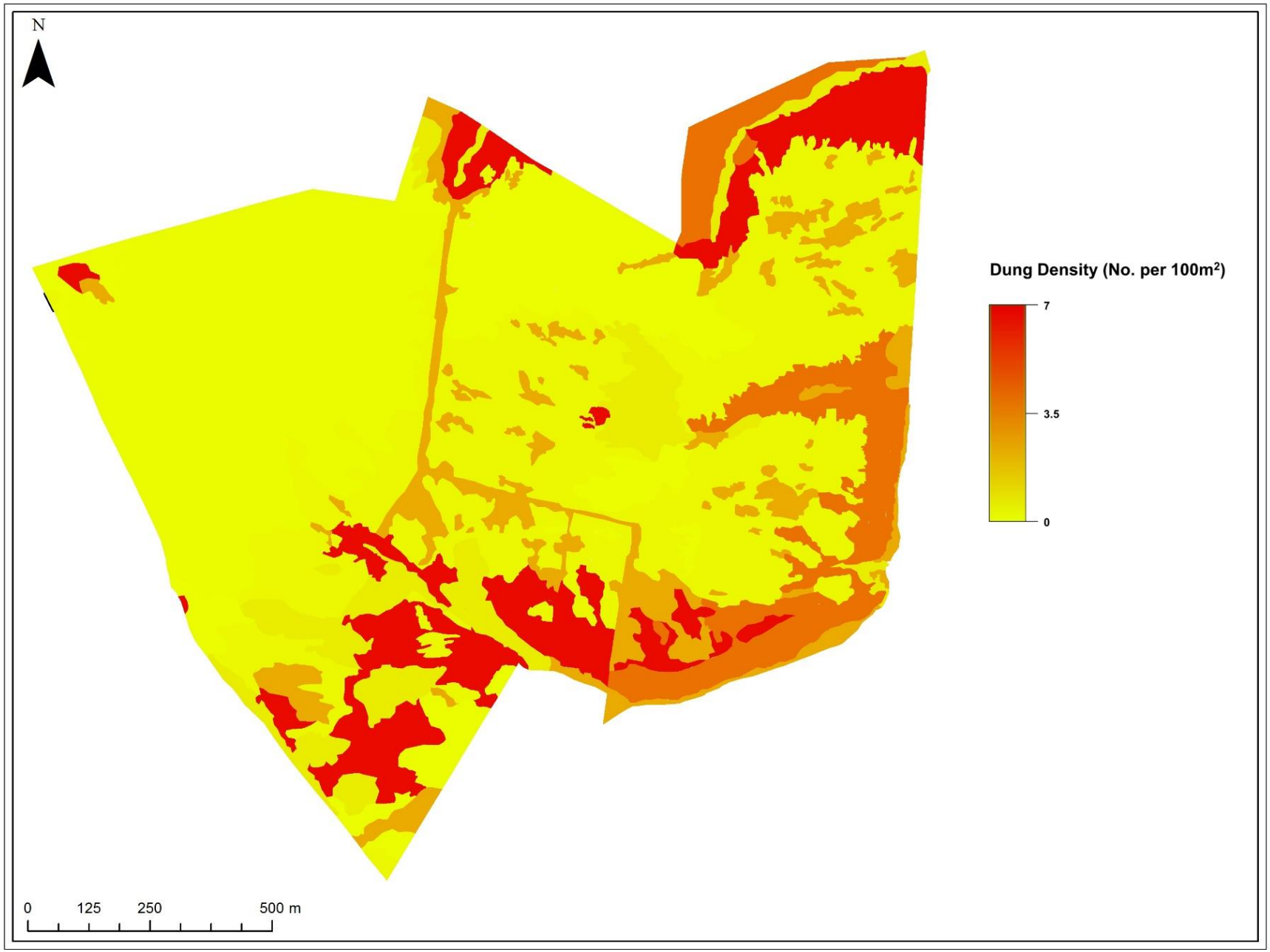


Figure 34: Map of Squallacombe and Aclands showing the estimated density of cattle dung in different areas based on the distribution of different habitat types and their estimated dung density.

4.3 Results

4.3.1 Dung density surveys

In July 2014 the distribution of cattle dung in different habitats did not differ significantly based on the area of each habitat surveyed ($\chi^2_6 = 6.04$, $p = 0.42$; Figure 30). However, by October 2014 the distribution of cattle dung in different habitats was significantly different ($\chi^2_6 = 59.69$, $p = 5.2 \times 10^{-11}$; Figure 31).

In July 2014 only two points recorded dung densities of ≥3 per 100m^2; one in an acidic grassland community, and another in a mix of wet *Molinia* and rush-dominated flush (Table 10). By autumn, 18 points recorded dung densities of ≥3 per 100m^2. High density points fell under a number of different habitat categories, with two different vegetation communities in each of the dry grassland, rush-dominated, *Molinia*-dominated, and transitional bog categories, and one community in the bracken-dominated and blanket bog categories (Table 10).

Surveying in the 2015/16 field season found a significant difference in the density of cattle dung in different habitats ($\chi^2_6 = 125.53$, $p = 2.2 \times 10^{-16}$; Figure 33). There was no significant difference in dung density between pre- and post-restoration habitats ($\chi^2_1 = 0.77$, $p = 0.38$)

In 2015/16, 45 points, spread between 11 different vegetation communities, recorded dung densities of ≥3 per 100m^2. Six of these vegetation communities fell under the dry grassland habitat category. Dung densities of ≥3 per 100 m^2 were recorded in two vegetation communities in the bracken-dominated and rush-dominated categories, with one community in the valley mire category (Table 11).

4.3.2 Timelapse camera surveys

Timelapse camera footage showed that neither the number of cattle recordings at each location ($\chi^2_{42} = 40$, $p = 0.56$; Table 12) or the number of days of recorded grazing ($\chi^2_{35} = 40$, $p = 0.26$; Table 12) were dependent on the amount of time a camera was left at the location.

4.4 Discussion

Cattle habitat use

There were significant differences in level of cattle usage between different habitats, with an apparent preference for drier areas. Cattle dung density was highest in vegetation communities of the dry grassland category, followed by bracken-dominated and then rush-dominated habitats. The wetter habitat types, including valley mire, *Molinia*-dominated, transitional bog and blanket bog, appeared to show little difference in dung density. Dung density in these habitats was fairly uniformly low, suggesting that cattle rarely spend much time in these areas. However, dung was recorded in all habitat categories, indicating that cattle do not avoid wetter areas entirely. The low densities may indicate either very low levels of grazing, or use of the habitats for transit as animals pass through in order to reach more favourable grazing areas. The level of selectivity demonstrated here could potentially be due to the large size of the study site and relatively small number of cattle, allowing animals to avoid unfavourable vegetation communities for grazing (Henkin *et al.* 2007; Probo *et al.* 2014).

The three high-use habitat types share a number of characteristics which may make them favourable for livestock. The dry grassland communities of the site are predominantly covered with graminoids and forbs, which are often selected by cattle for grazing (Lamoot *et al.* 2005; Putfarken *et al.* 2008). The homogeneous sward length and low density of unfavourable dwarf-shrubs and coarse grasses may allow cattle to feed indiscriminately. This is suggested as being particularly important for cattle, with areas containing large quantities of easily accessible, high-quality grazing reducing the need to exert fine-scale selection of forage species (Hodgson *et al.* 1991; Samuels *et al.* 2014). The dominant species in bracken and rush-dominated communities are likely to contribute to lower levels of cattle usage of these habitats, as neither is favourable for grazing. The high density of these species could therefore increase the time required for foraging within these habitats, as effort will be required to select favourable species and avoid the poor-quality dominants. Nevertheless, the understory communities in both of these habitats is similar to that of open dry-grass lawns, and can contain a high cover of fine-leaved

grasses. Thus, despite the high cover of low-quality species, there is an abundance of favourable forage species available, which could potentially explain the relatively high levels of cattle usage in both habitats.

Other factors may contribute to the lower levels of cattle use of these habitats. Level of cattle use in an area is negatively associated with the steepness of an area (Kaufmann *et al.* 2013), and as the bracken-dominated habitats are mainly situated on the sloping valley sides this could act as a deterrant. Rush-dominated habitats frequently occur as isolated patches within large areas of dense *Molinia*. As *Molinia*-dominated habitats appear to be less favourable for cattle, these rush patches may be visited less frequently as animals would have to transit through large areas of unfavourable grazing to reach them.

The less-usedhabitats also bear a number of similarities. All are dominated by coarse grasses, rush or dwarf-shrubs, but in contrast to the drier bracken-dominated and rush-dominated these dominant species are present at the exclusion of favourable species, rather than occurring alongside them. For example, where *Molinia* occurs at high density most other species are scarce or absent. Bog habitats may have a slightly higher cover of favourable forb or graminoid species, but the less favourable *Molinia*, dwarf-shrubs and bryophytes make up the majority of cover. This potentially means that, aside from the dominant species, potential forage species are scarce and thinly spread. As a result, cattle grazing these areas may have to spend a large amount of time selectively foraging in order to locate favourable species. While the dominant species may be used by cattle for grazing, they are typically less preferred than fine-leaved graminoids (Grant *et al.* 1987; Hodgson *et al.* 1991).

Aside from the poor foraging potential, other features of the wet habitats may make them unfavourable for grazing. Areas of waterlogged ground and open water could potentially make moving through these habitats more challenging. Furthermore, the large, robust tussocks of *Molinia* may further reduce accessibility when compared to the homogeneous, open lawns of dry grassland habitats. The key determinant of favourable grazing habitats appears to be a high cover of easily accessible, palatable forage species, with unfavourable grazing habitats exhibiting opposite characteristics.

Among favourable habitat categories, certain vegetation communities appeared to be used particularly heavily. For grassland habitats, the minerotrophic community, and acidic grassland with dry soft rush both appeared to be particularly favoured, with dung densities of ≥3 per 100 m^2 being recorded in ten and nine locations respectively. Rough grassland and *Deschampsia* grassland also appear to offer good grazing, with both recording densities of ≥3 per 100 m^2 despite few samples being taken due to the scarcity of the habitats on site. Other communities containing high dung densities included pure bracken, mixed bracken, bracken mixed with rush, pure acidic grassland, and rush mixed with dry grassland.

Examination of favourable grazing areas allows the identification of sward species that may contribute to cattle habitat selection. Favourable communities often contain a high cover of fine-leaved grasses, including *Agrostis* spp., *Festuca ovina*, *Anthoxanthum odoratum*, and *Holcus lanatus* (Chapter 3.2.1). As cattle typically feed more commonly on graminoids (Lamoot *et al.* 2005; Kingery *et al.* 2008; Putfarken *et al.* 2008) it is possible that it is the presence of such species which acts to attract cattle to these areas. While rough and *Deschampsia* grassland communities include relatively few fine-leaved grasses, both contain high cover of *Deschampsia cespitosa* which appeared to be heavily grazed on site (pers. obs.), possibly explaining the high use of these communities. As reported by Grant *et al.* (1996) Presence of *Nardus stricta* does not appear to be a deterrent where there is a reasonable cover of favourable species, as cattle will be able to select higher quality forage from among *Nardus* tussocks. However, cattle are likely to avoid areas where *Nardus* is dominant as they may struggle to obtain suitable quantities of favourable forage species (Grant *et al.* 1985) and high levels of *Nardus* in the diet may be detrimental to animal health (Common *et al.* 1998).

The disparity in habitat use could potentially result in ecosystem change. Overgrazing in upland pastures is a common problem, resulting in damaging processes such as soil erosion which may negatively impact upon a site's grazing value, and on ecosystem function as a whole (Evans 1997; Sansom 1999; Bilotta *et al.* 2007; Brazier *et al.* 2007). Stocking density is relatively low on the study site at ca. 0.2 cows per ha, compared to typically two cows per ha in lowland dairy farms (Chesterton 2009). However, as cattle activity is

concentrated within a small number of habitats, the impacts of grazing will not be spread evenly over the site. While grazing does not appear to be having a significant impact on high-use habitats at present, there would be potential for this to change were stocking densities to be altered.

The only wetter location with a dung density of ≥3 per 100 m^2 was in a patch of soft-rush dominated mire. The sampling point was close to areas of favourable habitat, and it seems likely that cattle used this particular location due to its proximity to preferred grazing areas.

Repeat surveys around the main catchment area appear to suggest that habitat use differs depending on season. Earlier in the season, cattle activity appeared to be relatively even between habitats, but as the season progresses, differences between different habitats emerged. Differences in seasonal habitat use, based on the availability of favourable forage species have been reported previously in cattle (Willms & Rode 1996), including in upland pastures (Grant *et al.* 1987). The key change appears to be a disproportionately high use of areas of bracken-dominated, dry grassland and rush-dominated habitats, and a disproportionately low use of *Molinia* and transitional bog habitats in late summer.

This change may perhaps reflect seasonal differences in the quality of different habitats. In spring, fresh growth of *Molinia* and bog plants are likely to offer reasonable quality grazing, meaning that wetter habitats are used more frequently. Indeed, in this season it appears that these habitats might be being grazed as frequently as dry grassland habitats. Nutritional quality of different vegetation communities seems to be relatively uniform at this time of year (Chapter 3.3.2), which may help to explain the higher levels of use of apparently unfavourable habitats. Furthermore, grazing fresh, early season growth of *Molinia* has been found to produce adequate levels of animal performance in cattle (Critchley *et al.* 2008; Fraser *et al.* 2011). Wetter habitats may be relatively productive during these periods due to the availability of large quantities of herbage mass from the growth of *Molinia*. In contrast, open grass lawns will offer fairly low quantities of forage earlier in the season until grass growth rates increase, potentially making it challenging for cattle to obtain suitable levels of intake.

As the season progresses, it appears that cattle visit wetter habitats considerably less frequently, preferring to spend more time in dry grassland, bracken-dominated or rush-dominated habitats instead. This may be due to differences in the rate of maturation between swards. *Molinia* shows a notable decline in quality towards the end of the growing season (Chapter 3.3.1), and as it is a dominant species in a number of the wetter vegetation communities this decline may act to deter cattle from using these areas for grazing. While other species are present, these frequently occur at low density among large areas of *Molinia*, making it inefficient for cattle to selectively graze any favourable species within these habitats (Critchley *et al.* 2008). As fine-leaved grasses and forbs, which dominate the drier habitats, do not show such a dramatic decline in quality with seasonality (Chapter 3.3.1), their relative value will increase as the season progresses. While other studies have noted an increase in the use of woody, shrub-dominated communities late in the season (Menard *et al.* 2002) as the availability and quality of graminoids declines (Grant *et al.* 1987), this was not apparent in the current study. It is possible that cattle are not grazed on the moor for long enough for a switch to dwarf-shrubs to be necessary; if animals were left on site for the whole of winter their use of blanket bog may increase.

These changes again appear to suggest that availability of favourable forage is the key factor determining level of cattle usage in an area. Furthermore, the results highlight the possibility that the value of different habitats will vary throughout the year. While *Molinia* and bog habitats may be used infrequently overall, they could potentially be of greater value earlier in the season. Therefore, although they offer poor quality grazing as vegetation matures, these habitats do still appear to offer some grazing value and maintenance of these habitats will ensure the availability of reasonable quality, fresh growth early in the season when cattle are first put out to graze.

Timelapse cameras recorded differences in levels of cattle usage in different habitat types, independent of differences in the length of time cameras were left at each of their locations. Frequency of recorded grazing was similarly not dependent on the number of recording days in the different locations. Observing animal behaviour from the timelapse camera showed that grazing was only observed in drier habitats, including dry grassland and bracken-dominated

areas. Animals were recorded in areas of *Molinia* and transitional bog, but only in transit. These findings support the results of the dung density surveys and the results of Grant *et al.* (1987), suggesting that cattle use drier habitats for grazing and spend little time in wetter areas due to poor grazing quality. However, timelapse surveys were only carried out relatively late in the season, and it's possible that surveys at different times of year may reveal greater use of, and evidence of grazing in, wetter habitats (Grant *et al.* 1987), as reported in sheep grazing systems (Welch 1998; Fraser *et al.* 2009; Williams *et al.* 2010).

Of note, at the start of the timelapse survey period animals had access to an adjacent improved pasture containing good cover of *Lolium perenne* and *Trifolium repens*. When this pasture was available animals spent very little time on the moorland pasture. Indeed, even the areas of relatively favourable minerotrophic grassland that were present immediately over the boundary of the two meadows were seldom used while the improved sward was available. Perhaps unsurprisingly, this would suggest that cattle will select *Lolium/Trifolium* swards where available in preference to semi-improved rough grazing, likely due to the higher productivity of such habitats (Common *et al.* 1991; Fraser *et al.* 2007; Fraser *et al.* 2009; Fraser *et al.* 2013).

These findings provide an indication of the habitat usage of one herd of cattle on one site, but further work would be desirable to confirm that these results are applicable elsewhere. It is possible, for example, that different breeds of cattle may use different habitats, or that habitat usage is affected by the density of grazing animals on a pasture. Study of levels of habitat usage across a number of different sites from a number of different regions would be valuable in determining broad patterns of grazing behaviour in cattle. It would also be valuable to begin monitoring dung density in all habitats at the start of the grazing season, and continue regularly until cattle are removed from the moor. This would provide a better indication of temporal variation in habitat usage, and could potentially reveal that the results reported here are not consistent throughout the year.

The effect of peatland restoration on cattle grazing

The results suggest that, at this site, the effect of peatland restoration on grazing value should be minimal. Both the 2014 dung density surveys and timelapse surveys suggest that little grazing occurs within the main catchment area. As this central catchment area contains the highest concentration of drainage ditches, it is the area likely to be most heavily affected by restoration. The change expected to occur will be a shift from *Molinia*-dominated communities around the drainage ditches to bog communities as species favouring wetter conditions recolonise (Haapalehto *et al.* 2010; Bellamy *et al.* 2011; D'Astous *et al.* 2013; Menberu *et al.* 2016). However, low densities of dung in both of these habitats, and in the catchment area as a whole, would suggest that a change in the prevalence of either habitat will not affect levels of cattle use as the area is rarely visited anyway.

Results of the 2016 dung density survey show that there is no significant difference between dung density in pre- and post-restoration habitats, with both *Molinia*-dominated and bog habitats seldom being used. As a result, a change in their relative extent should not have a major effect on grazing. As suggested previously (Wilson *et al.* 2011), this would imply that peatland drainage alone is not an effective means of improving grazing quality, as the resulting *Molinia*-dominated habitat is rarely used by livestock while other habitats are available. The vast majority of cattle activity is concentrated in drier habitats, and as these are unlikely to be affected by rewetting, restoration should not have any major effect on the productivity of a site of a site.

There is perhaps potential for a slight decrease in grazing value if isolated patches of favourable habitat are lost following rewetting. Within the large areas of *Molinia* and transitional bog there are small patches of dry grassland, and graminoid-rich rush-dominated areas; indeed, rush-dominated communities have typically developed along the lines of any drainage cuttings. These habitats contain good cover of apparently favourable species, and could therefore be selected for grazing by cattle. As they are usually surrounded by areas of *Molinia* or bog, there is greater potential for rewetting to affect them than there is in the larger blocks of favourable habitat on the periphery of the catchment. These communities are vulnerable to invasion by larger, coarser graminoids (Hulme *et al.* 1999), and if rewetting results in a rise in the water

table then succession may lead to these communities being dominated by *Molinia,* which favours wetter conditions (Hill *et al.* 1999). However, while these patches are used for grazing when encountered by cattle, perhaps when they are transiting between favoured grazing areas, they are unlikely to make a large contribution to the grazing value of a site as a whole. Grazing in these patches is likely to be opportunistic, and therefore their loss should have little effect on cattle foraging. Furthermore, grazing by livestock has the potential to prevent succession in these areas by preventing colonisation of dominant species and maintaining high levels of nutrient input through dung deposition (Hulme *et al.* 1999).

These findings are likely to be applicable to other areas with a similar mix of habitats, as is typical of British uplands. However, it is unclear how cattle would behave if placed on a pasture composed entirely of *Molinia*-dominated or bog habitats, and previous studies have either focused on the potential for cattle to graze one of these habitats (Grant *et al.* 1996; Grant *et al.* 1987; Critchley *et al.* 2008; Fraser *et al.* 2011), or, as in the current study, cattle habitat use in a mosaic of different vegetation communities (Hodgson *et al.* 1991). There appears to be little difference in levels of use between these habitats when more favourable grazing is available, but if animals were forced to use them it is possible that a stronger preference for one or the other may be displayed. It might be expected that cattle would favour *Molinia*-dominated habitats in spring when there is fresh regrowth of a reasonable quality, and bog areas later in the summer due to the presence of dwarf-shrubs which maintain similar levels of quality throughout the year, unlike *Molinia* which shows a major decline with season. In any case, the use of such pastures for cattle grazing would likely result in unacceptably low animal performance, hence why pastures used for cattle grazing almost invariably include at least some improved areas.

Conclusion

The results demonstrate that the distribution of different habitats will influence the distribution of cattle activity on sites with heterogeneous vegetation communities. It is likely that the key factors influencing habitat selection are quality and palatability of forage, although abiotic factors such as wetness and steepness may also play a role. The apparent preference for fine-leaved grass lawns, and grass rich bracken and rush dominated habitats, supports the

findings of previous studies which suggest cattle will select high-quality graminoid rich areas over scrub or dwarf-shrub communities. These findings have implications for conservation grazing as a management technique, as vegetation communities targeted for management will not necessarily be affected by cattle if there are more favourable grazing areas present.

This study appears to provide an example of a case where ecosystem restoration will not have a detrimental effect on existing land uses. As agriculture is one of the most significant land uses, and ecosystem restoration is increasingly used as a means of improving the functionality of degraded agricultural land, it is noteworthy that this need not necessarily affect the profitability of farming in terms of the grazing value of the land. Some interventions aimed at improving land for grazing appear not to have offered an improvement over the habitats that would have originally been present. While this will be extremely variable depending on the habitat studied, peatland restoration appears likely to result in a shift from one unfavourable grazing habitat to another, thereby having a minimal impact on grazing value as a whole.

However, the results of this study demonstrate that habitats are not equal in terms of grazing value, which highlights the potential for ecosystem change to affect grazing systems. Habitats are sensitive to any changes in abiotic and biotic processes, with the potential for variations in any of these processes to drive change in the extent and distribution of certain habitat types. As grazers exhibit preferences for particular habitats, ecosystem change could have a knock on effect in cases where the area of favoured grazing is affected. If the new habitat is similar in terms of grazing value then this is likely to have a minimal effect, but where the replacement vegetation community is of a lower quality it is likely to be detrimental to grazing animals. As a result, there is clearly possible for ecosystem change to influence grazing, with potential to affect the fitness of wild herbivores, and the profitability of agriculture in pastoral farming systems.

Chapter 5: Parasite populations in upland pastures

5.1 Background

5.1.1 Infectious disease and ecosystem change

Globally, a number of diseases are showing changes in their distribution, with their emergence in new regions posing a significant threat to humans (Gubler 1998; Morens *et al.* 2004; Jones *et al.* 2008). Aside from the obvious threat to health, emerging diseases may also affect human life by reducing food production through the infection of livestock (Purse *et al.* 2005; Babiuk *et al.* 2008) or crops (Anderson *et al.* 2004). As pathogens, parasites and vectors may all be affected by characteristics of their environment, ecosystem change has great potential to alter the spread of disease in a wide variety of ways (Daily & Ehrlich 1996; Patz *et al.* 2000).

Climate change is a key driver of change in ecosystems, and as a result it could affect the emergence of infectious diseases in numerous ways (Patz *et al.* 1996). Rising temperatures associated with global warming may directly affect the abundance of pathogens and parasites, for example, by increasing their developmental rate and decreasing their incubation period, resulting in increased infection rates in host species (Patz & Olson 2006; Poulin 2006; Paull & Johnson 2010). However, climate change may perhaps have a greater influence on the spread of disease through its effect on the distribution and abundance of vector and host species. Again, rising temperatures have the potential to drive major changes in the populations of vectors such as mosquitoes (Pascual *et al.* 2006). As the distribution of many species is limited by climatic variables such as temperature, warmer conditions may drive shifts beyond the boundaries of endemic areas, and increase the prevalence of disease in cooler areas such as those at higher altitude (Martens *et al.* 1995; Siraj *et al.* 2014). As with pathogens, temperature may also affect the development of vectors. Increases in temperature may result in increased breeding productivity of vector species (Paull & Johnson 2010), which could potentially increase the local risk of infection.

Water availability is another major factor determining the distribution and abundance of vectors of a number of significant diseases. Climate change may have a direct

impact on this, as an increasingly intense hydrological cycle will affect precipitation rates, which may in turn affect the spread of water-borne and vector-borne disease (Epstein 2001; Chen *et al.* 2012). Numerous invertebrate vectors, including dipterans and molluscs, require standing water to complete their lifecycle. Thus, if water bodies are created in areas where they were previously absent, either through increased precipitation or the creation of artificial water sources by humans, vectors may be able to colonise new areas (Gates & Boston 2009; Sang *et al.* 2017). Humans have had a major impact on the distribution of standing water on the land surface, with irrigation of arid areas allowing malaria-vector mosquitoes to persist in regions where previously they would have only occurred sporadically following suitable rainfall events (Tyagi 2004; Baeza *et al.* 2011).

Characteristics of water bodies may also be important, and therefore human-driven processes such as damming and eutrophication may affect populations of hosts and vectors (Norris 2004; Johnson *et al.* 2010). For example, different mosquito species may show fine-scale habitat preferences based on features of a water body such as whether it is still or flowing, and clear or turbid; as a result, where conditions become unsuitable for one species they will often become favourable for another, with little change in overall disease risk (World Health Organisation 1982).

Changes in the distribution of host species may affect the prevalence of vectors and pathogens. Urbanisation is recognised as a key driver of changes in the distribution of disease, with, among other factors, a dense concentration of hosts providing a reservoir for pathogens and acting to attract vectors such as mosquitoes (Rochlin *et al.* 2016; Hassell *et al.* 2017). Settlement by humans in a new area, or movement of vectors through natural range expansion or accidental importation, may similarly lead to disease outbreaks as pathogens may come in to contact with hosts which are lacking any form of resistance (Marques *et al.* 1987; Mack *et al.* 2000; Mazza *et al.* 2013). Aside from acting as a food source, humans moving in to a new area will often bring livestock, which may alter the distribution of blood-feeding arthropod vectors leading to aggregations around settlements (Mayagaya *et al.* 2015; Rogalski *et al.* 2016)

Vectors may be affected by changes in vegetation characteristics. Some plant species can directly facilitate colonisation by vectors, with species that trap water in

their leaves providing breeding sites for dipterans (Downs & Pittendrigh 1946). Different species will show preferences for different levels of vegetation cover (World Health Organisation 1982), and therefore vector populations may be affected, either positively or negatively, by clearance of vegetation or changes in community structure. In mosquitoes, interspecific differences in habitat preferences can mean that the planting of crops or forest results in a change in their species composition and abundance (Warburg *et al.* 1991; Chang *et al.* 1997).

Habitat degradation and ecosystem simplification may be associated with an increase in disease risk (Foley *et al.* 2005). For pathogens with multiple hosts, intact ecosystems have the potential to dampen the risk of infection in humans by supporting a diversity of alternative hosts (Ostfeld & Keesing 2000; Ezenwa *et al.* 2006; Keesing *et al.* 2010). Where the structural complexity of an ecosystem is lost, for example through deforestation, vectors may profit if they are able to survive in the new landscape. As deforestation may coincide with the arrival of new hosts in the form of humans and livestock, and new breeding sites in artificial water sources, vector populations may expand and disease outbreaks may occur (Molyneux 2003; Kilpatrick & Randolph 2012). Improved transport links and mobility of humans further allow vectors and pathogens to be spread widely to new areas (Patz *et al.* 2004).

5.1.2 Infectious disease and livestock

Infectious diseases pose a threat to livestock health, and can therefore threaten food security and the economic viability of agriculture in worst affected areas (Tomley & Shirley 2009). Individual diseases may place major constraints on the productivity of farming in developing regions, as demonstrated by the viral disease peste des petits ruminants, which is endemic to parts of Africa, the Middle East and the Indian subcontinent (Jones *et al.* 2016; Mariner *et al.* 2016). Global change has resulted in the emergence of newly recognised diseases in livestock, and lead to changes in the distribution and prevalence of known diseases (George 2008).

Table 13: the estimated cost to the UK agriculture industry of various vector-borne and parasitic diseases. Figures obtained from (1) Alarcon *et al.* 2014; (2) Defra 2002; and (3) Niewhof & Bishop 2007

Disease	Species	Vector/parasite	Livestock	Estimated cost
Blowfly Strike	Dipteran spp.	Parasite	Sheep	£2.2m[2]
Coccidiosis	*Eimeria* spp. (protozoan)	Parasite	Poultry	£12.6m[2]
Fasciolosis	*Fasciola hepatica* (trematode)	Parasite	Cattle	£23m[2]
Gastro-intestinal parasites	Nematode/trematode	Parasite	Sheep	£84m[3]
Infectious bovine keratoconjunctivitis	Dipteran spp.	Vector	Cattle	£11.9m[2]
Parasitic bronchitis	*Dictyocaulus viviparous* (nematode)	Parasite	Cattle	£9.5m[2]
Schmallenberg Virus	*Culicoides* spp (dipteran)	Vector	Sheep	£6.40-20.85 per ewe[1]
Sheep Scab	*Psoroptes ovis* (mite)	Parasite	Sheep	£8m[3]
Toxoplasmosis	*Toxoplasma gondii* (protozoan)	Parasite	Sheep	£12.4m[2]

A Defra estimate of the cost of 35 significant livestock diseases amounts to £285.1m per year based on produce losses alone (2002), and among diseases of economic importance there are a number which are vector-borne or parasitic (Table 13). However, it can be challenging to determine the economic impact of disease in livestock. Calculating a value is complicated by the numerous ways in which disease may cost farmers, including reduced health or mortality of animals, lower quality or

quantity of produce such as milk, reduced reproductive success, expenditure on vaccination or treatment, and delayed costs such as those related to market disruption (Pendell *et al.* 2016; Saatkamp *et al.* 2016). Different diseases will cause losses through varying combinations of these factors, and as each factor will affect the economic value of a disease differently establishing the actual cost is complex (Chi *et al.* 2002). The cost of a disease may show great variability between different farming regions, even those in relatively close proximity, and therefore costs need to be evaluated at a relatively fine-scale resolution to identify areas which are most heavily affected (Raboisson *et al.* 2014; Nampanya *et al.* 2016).

Furthermore, at times it is difficult to establish the value of controlling a disease. Eradication of a disease in an area may involve the removal of infected animals and therefore results in direct economic loss, but this may be greatly outweighed by the benefit of increased production in the future (Stott *et al.* 2012). Effective control may be reliant on widespread implementation in a region, which may be difficult in poorly-developed areas where treatments may be prohibitively expensive (deCastro 1997). The relative value of intervention may also vary between regions, depending on prevalence of the disease and the income of local people, making it challenging to implement wide-scale, consistent treatment methods (Shaw *et al.* 2014). As a result, it may be more effective to introduce measures to reduce the risk of numerous diseases at once, rather than only focussing on treating immediate threats (Cowie *et al.* 2014).

Control is further complicated in semi-natural or natural pastures. Reservoirs for disease may be found in wild animal populations of natural habitats (Bengis *et al.* 2002; Gortazar *et al.* 2007; Miller *et al.* 2013), and therefore even if eradicated from livestock herds, animals will be susceptible to infection when coming in to contact with wildlife or grazing natural rangelands (Scasta 2015). Culling of wild animals is sometimes used in attempt to control wildlife-livestock transmission of disease; however, this approach may have unintended consequences, with culling of badgers in the UK resulting in increased transmission of bovine tuberculosis in areas surrounding culling sites (Carter *et al.* 2007; Donnelly *et al.* 2012) While a disease may be deemed to be eradicated from a region, it can quickly re-emerge if still present in surrounding areas, highlighting the need for continual vigilance (Carabin *et al.* 2014).

5.1.3 Tick-borne diseases

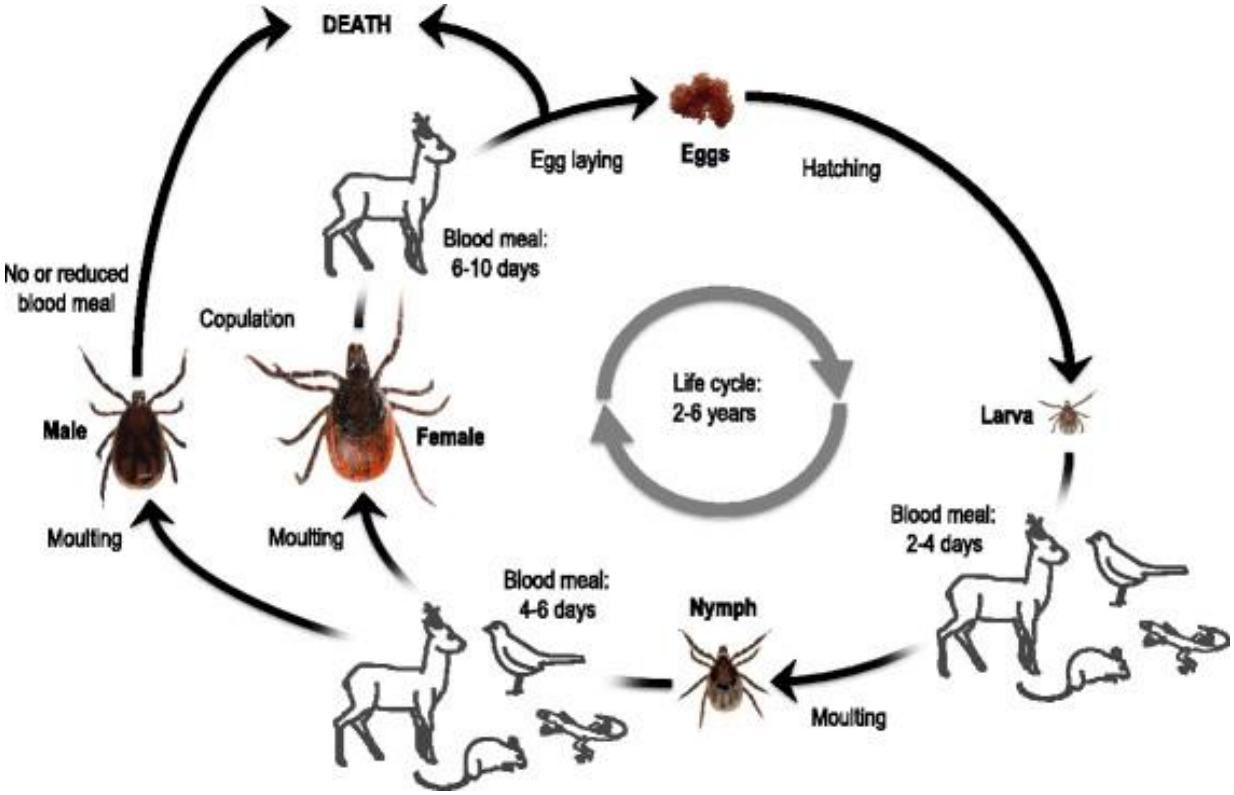
Globally ticks are important vectors for a number of pathogens, some of which pose a significant threat to human health (Jongejan & Uilenberg 2004). In Europe, tick-borne diseases of importance include Lyme borelliosis and tick-borne encephalitis, with both occurring relatively frequently within the region (Randolph 2001; Charrel *et al.* 2004). There is evidence of increased incidence of these diseases in Europe, possibly associated with changes in the distribution of vectors due to climate change (Gray *et al.* 2009; Millins *et al.* 2016). Rising temperatures are predicted to increase tick abundance and the incidence of tick-borne disease, as warmer conditions may increase the questing season and increase the distribution of favourable habitats and hosts (Jaenson & Lindgren 2011). However, climate change is unlikely to be the sole reason for increasing incidence of tick-borne disease, with higher reporting rates and increases in host abundance likely to be playing important roles (Randolph 2004; Schwarz *et al.* 2009; Medlock *et al.* 2013;).

In addition to the threat posed to human health, a number of tick-borne diseases are responsible for reduced health and mortality in livestock. The effects of tick-borne diseases on livestock may be most damaging in poorly-developed countries where a reduction in productivity may represent a major loss of income for local farmers (Minjauw & Mcleod 2003; Kivaria 2005). Diseases of economic importance include louping ill (Brodie *et al.* 1986) and babesiosis (Beugnet & Moreau 2015), with different pathogens affecting different species of domestic animal.

Ixodes ricinus is the most widespread and abundant tick in the UK, and acts as a vector for a number of diseases of medical and economic importance (Pietzsch *et al.* 2005). The life cycle of *I. ricinus* involves 3 different hosts as the tick develops from larvae, to nymph, to adult (Figure 35). Among other diseases, *I. ricinus* is the vector of bovine babesiosis, a significant disease in the cattle industry usually caused by the pathogen *Babesia divergens* (L'Hostis *et al.* 1995). The seasonal occurrence of bovine babesiosis is closely linked to the seasonal pattern of *Ixodes ricinus* activity (L'Hostis *et al.* 1995). Bovine babesiosis results in loss of condition due to fever, anorexia, anaemia and depression of feeding activity (Zintl *et al.* 2003). In severe cases the disease is deadly, with an estimated 10% mortality rate from cattle herds in Ireland in 1983 (Gray & Harte 1985). While clinical signs of the disease may

appear relatively infrequently, its serological prevalence may be much higher (L'Hostis & Seegers 2002). Cattle appear to be most susceptible when naïve adults are introduced to an area where bovine babesiosis is endemic without having had the chance to develop resistance as juveniles (Everaert *et al.* 2007). The disease can place constraints on the cattle farming industry where common, although in areas where agricultural practices have decreased habitat suitability for ticks its incidence is decreasing (Zintl *et al.* 2014; Zintl *et al.* 2017). Models suggest that increasing deer density increases the likelihood of infection in cattle, while use of acaricides decreases the prevalence of the disease (Hoch *et al.* 2012).

Figure 35: a diagram of the life cycle of *Ixodes ricinus*, taken from Herrmann & Gern 2015.



5.1.4 The ecology of Ixodes ricinus

The density of *I. ricinus* may vary between different habitats, and thus it will occur at different densities across a landscape. In open habitats such as pasture land, the presence of woodland or tree cover is associated with an increase in tick abundance (Boyard *et al.* 2011; Dobson *et al.* 2011; Kiewra *et al.* 2017), which may be due to

the associated higher humidity when compared with unsheltered pastures (Boyard *et al.* 2007). Indeed, where tree encroachment on pasture occurs the risk of tick bite will increase significantly (Gilbert *et al.* 2017). As a result, the removal of tree or scrub cover, for example through forest clearance or the conversion of plantations to peatland, is suggested as a means of reducing the tick density of an area (Hubalek *et al.* 2006; Gilbert 2013; Tack *et al.* 2013). Different woodland types differ in their suitability for ticks, with deciduous supporting higher densities than coniferous, and high understorey cover supporting higher densities than low cover (Estrada-Pena 2001; Tack *et al.* 2012a; Tack *et al.* 2012b; Ceballos *et al.* 2014). *Ixodes ricinus* may be absent from open habitats and areas of homogeneous coniferous woodland (Estrada-Pena 2001), and where present in open habitat types the type of vegetation cover is important with, for example, heather supporting smaller populations than dune vegetation (Wielinga *et al.* 2006). Cover is important in pastures, and thus the species is frequently found in rough moorland pastures, but may be absent from closely grazed, intensively managed lowland pastures (Milne 1950a). Microhabitat characteristics can influence the fine-scale distribution of questing individuals, with aspects such as topographical features for shelter from temperature extremes, and higher soil moisture acting to promote higher tick abundance (Medlock *et al.* 2008).

Ixodes ricinus typically exhibits a bimodal activity pattern, with a large peak in spring and early summer followed by a smaller one in early autumn (Schwarz *et al.* 2009). However, in some habitats and regions a unimodal pattern of activity may exist, related to factors such as sunshine duration, temperature, precipitation, air humidity, and altitude (Craine *et al.* 1995; Buczek *et al.* 2014; Qviller *et al.* 2014; Schulz *et al.* 2014). Weather patterns may dictate tick abundance in any given year, with factors such as mean winter temperature having an impact on tick survival and thus population size in the following year (Lauterbach *et al.* 2013). The effect of weather on tick abundance may not be immediate, with effects appearing months or years later resulting in large inter-annual fluctuations in tick population size (Paul *et al.* 2016) which may lead to different habitat types supporting the highest tick densities in different years (Bisanzio *et al.* 2008). Humidity performs well as a predictor of tick distribution, and the factor is of high importance as questing individuals may be vulnerable to desiccation when the saturation deficit is high (Alonso-Carne *et al.* 2015). Indeed, experiments suggest that *I. ricinus* will not survive if relative humidity

is lower than 70-80% (MacLeod 1934, 1935; Milne 1950b). Periods of low humidity early in a season appear to reduce tick abundance later in the year, presumably due to direct mortality of adult ticks (Berger *et al.* 2014). Temperature is also potentially an important factor in determining levels of tick questing, meaning that topographical features such as aspect and altitude of a site will affect tick population size and activity (Qviller *et al.* 2014; Kazimirova *et al.* 2016). While rising temperatures promote tick activity in spring, beyond a certain point high temperatures will reduce tick questing (Nelson *et al.* 2015), presumably due to the increased risk of desiccation. However, humidity appears to be of greater importance than temperature in influencing tick activity, and effects of temperature on tick activity may actually be driven primarily by associated changes in humidity (Buczek *et al.* 2014).

As well as habitat characteristics, host density may have a major influence on tick density. In the UK deer are important wildlife hosts of *I. ricinus*, and the density of questing ticks is closely associated with the level of deer activity in an area (Jensen *et al.* 2000; Ruiz-Fons & Gilbert 2010; Qviller *et al.* 2016). Indeed, levels of host use are likely to be an important driver behind differences in tick density in different habitats, such as deciduous and coniferous woodland (Tack *et al.* 2012). Where deer are culled, or excluded from an area by fencing, ticks may occur at significantly lower densities (Gilbert *et al.* 2012). In addition, the presence of livestock may reduce tick numbers by reducing the density of deer through competitive exclusion (Steigedal *et al.* 2013), and creating vegetation communities which are unfavourable for other wild host animals such as rodents (Gassner *et al.* 2008). Rodents are of particular importance as hosts during the nymphal stage, and as particular species may be more favoured by *I. ricinus* the diversity and relative abundance of different rodent species will have an effect on tick density (Perez *et al.* 2016). Where favourable alien mammals are present they may become more highly used than native host species, thus supporting higher tick populations than may naturally occur (Craine *et al.* 1995). As well as affecting population size, host animals may also facilitate dispersal of *I. ricinus*, with colonisation of new habitat patches being heavily reliant on movement of host animals from areas of high tick density (Estrada-Pena 2003).

The proportion of infected individual ticks in a population shows high temporal and spatial variation based on factors such as climatic variables, including temperature (Millins *et al.* 2016) and habitat characteristics (Hamsikova *et al.* 2016). Levels of

infection in *I. ricinus* appear to be positively associated with density of rodents in a habitat, with these acting as a reservoir for a number of different pathogens (Halos *et al.* 2010).

5.1.5 Fasciolosis and Galba truncatula

The liver fluke *Fasciola hepatica*, cause of fasciolosis, is a trematode with a complex life cycle requiring development in an intermediate host, with large mammals including humans used as a definitive host (Roberts 1950). Fasciolosis is a significant and increasing problem in European farms, and it continues to emerge in areas where it was previously scarce or absent (Mitchell 2002; Pritchard *et al.* 2005; Knubben-Schweizer *et al.* 2010; Skuce & Zadoks 2013). Liver fluke causes poor health and production losses in cattle, and can occasionally be fatal (Mitchell 2002). Fasciolosis may result in economic losses through a number of routes, including reducing animal health, reducing the quality of produce, and increasing expenditure on antihelminthes and treatment (Saleha 1991). In the UK, gastro-intestinal diseases in sheep, including fasciolosis are estimated to result in losses of £84m per year, while in cattle the disease costs £23m per year (Table 13). The effect of Fasciolosis on an animal will vary depending on the level of infection, and while control appears to be relatively effective it can be challenging to implement (Kaplan 2001).

The snail *Galba truncatula* is the most important intermediate host of *F. hepatica*, although other snail species may be used occasionally (Caron *et al.* 2007; Relf *et al.* 2009; Caron *et al.* 2014). The proportion of infected individuals in a population is often very small, although the number varies between populations and seasons (Dreyfuss *et al.* 2005; Radev *et al.* 2008). *Galba truncatula* favours small water bodies such as ditches and ponds, and is commonly present in patches which are only seasonally wet or have fluctuating water levels (Hourdin *et al.* 2006; De Roeck *et al.* 2014). The snail is able to survive relatively long periods without water by burying in mud and remaining dormant until conditions become more suitable (Belfaiza *et al.* 2009). Snail numbers fluctuate seasonally, with either one or two generations per year depending on region (Belfaiza *et al.* 2005; Rondelaud *et al.* 2009). Variation in snail numbers leads to variation in the seasonal incidence of

fasciolosis in livestock, with animals being at risk following periods of high snail abundance (Novobilsky *et al.* 2014).

Galba truncatula exhibits fine-scale microhabitat preferences, with higher abundances associated with particular vegetation communities and plant species (Rondelaud *et al.* 2011; Charlier *et al.* 2014). While the species favours areas of higher water pH it is versatile and may be common in areas with acidic soil (Heppleston 1972; Rondelaud *et al.* 2011; Charlier *et al.* 2014). However, certain soil types may be avoided if microhabitat conditions are unfavourable; for example, peat appears to be unsuitable because it does not support the microalgal growth on which the snails feed (Heppleston 1972).

Galba truncatula has fairly poor dispersal capabilities, but may be able to migrate along water courses when conditions are favourable (Rondelaud *et al.* 2005). The seasonal behaviour of the snail may vary depending on region, with a higher proportion of individuals aestivating during dry spells in populations inhabiting areas with more ephemeral water bodies (Goumghar *et al.* 2001). Emergence of fasciolosis in new regions has been linked to changes in climate which may favour *G. truncatula*, for example through increases in summer rainfall (Pritchard *et al.* 2005). Climate change could also increase the incidence of fasciolosis by directly benefitting *F. hepatica*, with higher temperatures and extreme temperature variations increasing developmental rate and productivity (Bossaert *et al.* 1999; Rondelaud *et al.* 2013; Vignoles *et al.* 2014). Farm management practices have an effect on incidence rates of fasciolosis (Bennema *et al.* 2011), with decreased risk where management reduces habitat suitability for *G. truncatula* (Dreyfuss *et al.* 2016).

5.1.6 Hypotheses

This study focuses on two species of importance to livestock health: *Ixodes ricinus* and *Galba truncatula*. The following questions are examined:

1. Do different upland habitats differ in their populations of the selected species?

2. How will peatland restoration affect populations of the selected species in upland pastures?

In order to compare *I. ricinus* abundance in different habitat types, blanket drags were carried out across a number of different vegetation communities, and the number of ticks in each of these was counted. In an attempt to survey *G. truncatula* populations on the study sites, opportunistic surveys of suitable habitat were carried out during the species' peak season, involving careful searching of muddy areas and water bodies.As both species are known to exhibit preferences for particular micro-habitats, it is hypothesised that upland pastures will show spatial variability in the populations of *I. ricinus* and *G. truncatula* due to presence of a variety of different vegetation types. Furthermore, it is hypothesised that peatland restoration will alter the populations of these species in upland pastures as habitat change will affect their distribution and abundance.

5.2 Materials and methods

The study was carried out at four different sites: Hangley Cleave, Long Holcombe, Spooners, and the Squallacombe and Aclands site (descriptions in Chapter 2.2.1). These sites were selected due to the range of different vegetation communities present at each. Furthermore, each site is used for farming, and thus livestock are present throughout the grazing season. Hangley Cleave, Long Holcombe and Squallacombe and Aclands were grazed by cattle in both years of the study. In addition, Hangley Cleave, Spooners, and Squallacombe and Aclands were grazed by sheep in both years, and Spooners was grazed by a herd of Exmoor ponies. Wild red deer were observed on all sites.

5.2.1 Ixodes ricinus surveys

Tick population surveys were carried out in the summers of 2015 and 2016. It was intended that two surveys would be carried out on each site in each year, with the surveys being carried out approximately 2 weeks apart. Surveys on Aclands and Squallacombe were occasionally split between days, while on other occasions multiple sites were surveyed in a day. Due to access issues, only one survey could be completed at Long Holcombe in each year. Three surveys were carried out at Aclands and Squallacombe in 2016, as a second survey was abandoned early due to unfavourable weather conditions. Surveys were timed to coincide with high tick populations in spring and early summer, but were spread over a much greater period

in 2016 due to poor surveying conditions. Surveys in each round were intended to be carried out as close together as possible to minimise differences between sites, but again this was made difficult in 2016 due to the unfavourable weather. In 2015, the first round of surveys were started on May 28th and finished by June 8th, while the second round were started on June 23rd and finished on June 24th. In 2016, the first round of surveys were started on June 7th and finished on July 12th, while the second round were started on July 18th and finished on September 1st. The dates of all surveys carried out are provided in Table 14.

Table 14: Dates for all *Ixodes ricinus* surveys carried out over the two survey years.

	2015		2016		
Site	**1st survey**	**2nd survey**	**1st survey**	**2nd survey**	**3rd survey**
Aclands	28.05	23.06	07.06	19.07	01.09
Hangley Cleave	07.06	23.06	18.06	18.07	Na
Long Holcombe	08.06	Na	18.06	Na	Na
Spooners	04.06	24.06	12.07	09.08	Na
Squallacombe	07.06	23.06	07.06	19.07	01.09

To survey tick populations, blanket drags were carried out. This involved dragging a 1 m^2 sheet of cloth over vegetation, causing questing ticks coming in to contact with the sheet to latch on. If weather conditions were deemed likely to significantly suppress tick questing activity then surveys were not carried out; unsuitable weather would include low temperatures, high winds, and rain. Notes on weather conditions were recorded at the start of each survey. Surveys were carried out by walking across the site through various habitats, with the route of each walk being recorded by a GPS logger. The blanket was attached to a wooden pole and held out to one

side to reduce the risk of questing ticks attaching to the surveyor before coming in to contact with the sheet. The blanket was held in a way to try and maximise contact with vegetation, although the actual area of contact varied depending on habitat structure. The blanket was checked for ticks at intervals of 10-20 m along the walk. The number of individuals were recorded, before being removed from the blanket and released in the area just surveyed to prevent re-capture when the next section of the walk was carried out. The start and end point of each section of the walk was marked using the GPS logger (with accuracy to 5 m). A rough description of the habitat covered by each section was noted, and if a habitat boundary was encountered that section of the walk was ended before starting a new section in the new habitat type. The length and time spent on each walk varied depending on a number of factors, including size of the site, and the period of suitable weather during a day. However, on each survey, effort was made to cover a range of habitats on each site, and over both survey seasons the aim was to cover as many different parts of a site as possible.

5.2.3 Mapping tick density and tick-borne disease risk

Tick densities in different broad-scale habitat categories were used to create a heat map of tick abundance for the Squallacombe and Aclands site based on the previously created habitat map (Chapter 2.2.2). Densities for each habitat category were created for 2015 and 2016, and applied to the habitat map in an attempt to visualise the spatial distribution of *I. ricinus* on the site based on the distribution of different habitats. In order to map disease risk, habitat-based values for tick density were multiplied by those for cattle dung density (a proxy measure of cattle habitat use).

5.2.4 Statistical Analysis

Routes recorded by the GPS loggers were imported in to ARCmap, and the distance covered by each section of each route was calculated from the GPS log data. Sections of each route were assigned to one of seven broad-scale habitat categories based on field observations and habitat maps where available. Tick counts from all

sites were combined and used to create an estimate of tick density per m^2 based on the total number of ticks recorded in each habitat and the total area surveyed in each habitat. These results were then expressed as an estimate of tick density per km^2 in each habitat category. Separate densities were calculated for the 2015 and 2016 field season. A Kruskal-Wallis one-way analysis of variance was carried out to determine whether different habitats differed in the tick densities they supported in both the 2015 and 2016 field season. For 2016, separate analyses were carried out including and excluding the additional Squallacombe and Aclands survey day. This was due to the fact that the additional survey recorded a large number of ticks but only sampled a small subset of habitats, and thus may not have allowed a representative comparison of tick density in different habitats on that day.

In addition, a Kruskal-Wallis one-way analysis of variance was carried out to determine whether tick density differed between pre- and post-restoration habitats. This analysis combined the results of the 2015 and 2016 surveys, with the pre-restoration category including all *Molinia*-dominated habitats, and the post-restoration category including all transitional bog and blanket bog habitats.

5.2.5 Galba truncatula surveys

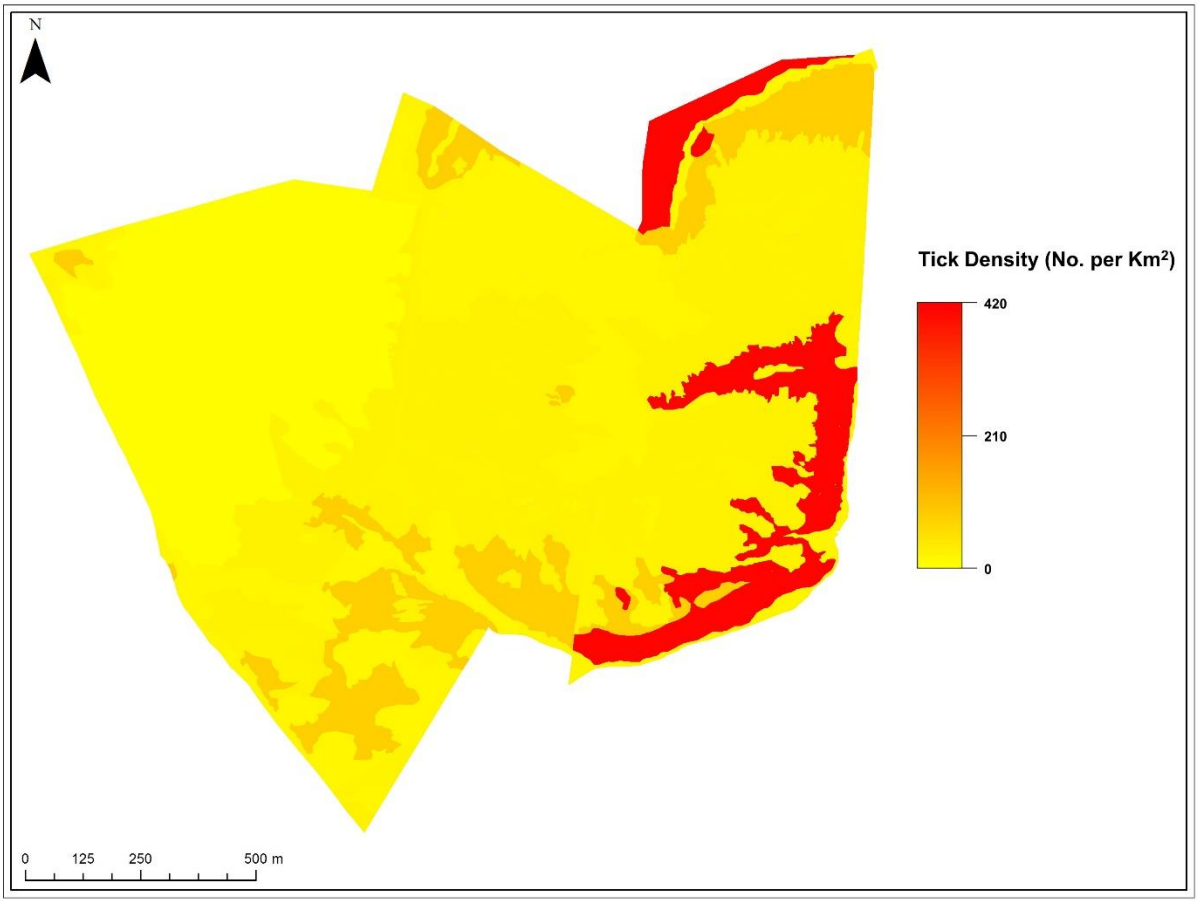
Surveying for *G. truncatula* involved opportunistic sampling and targeted surveys on the Squallacombe and Aclands site. Surveys were carried out sporadically between 2012 and 2016 between May and September to coincide with peak periods of snail activity. A pilot study involved the searching of a variety of areas within the main catchment areas of Aclands, with survey locations being marked and carefully checked for the presence of snails (Hazel Kendall pers. comm. 2013). Subsequent to this, searches were carried out on the Squallacombe and Aclands site and expanded away from the catchment area to include potentially suitable habitat in other parts of the sites and nearby areas beyond their boundaries. Surveyed areas included a variety of wetter habitats, such as drained and undrained peatland, bog pools, muddy pools and flushes in improved pasture, small moorland streams and the heads of larger rivers in the valley bottoms. During each visit, I searched sampling points for at least 30 minutes, and each sampling point was visited at least twice

over the course of the study, amounting to more than 20 hours of search effort. The location of all survey areas were recorded using a handheld GPS device.

Table 15: Area covered and number of ticks recorded at each site in the two study years.

Site	2015 Area covered (m^2)	2015 No. of ticks	2015 Tick density (No. per Km^2)	2016 Area covered (m^2)	2016 No. of ticks	2016 Tick density (No. per Km^2)
Aclands	4145.16	304	7.33	3286.1	115	3.5
Hangley Cleave	3183.97	41	1.29	2407.65	52	2.16
Long Holcombe	1589.47	82	5.16	1046.21	22	2.1
Spooners	4450.89	110	2.47	3549.91	170	4.79
Squallacombe	3120.85	20	0.64	2532.56	16	0.63
Total	16490.34	557	**Mean:** 3.38	12822.4	375	**Mean:** 2.92

A.



B.

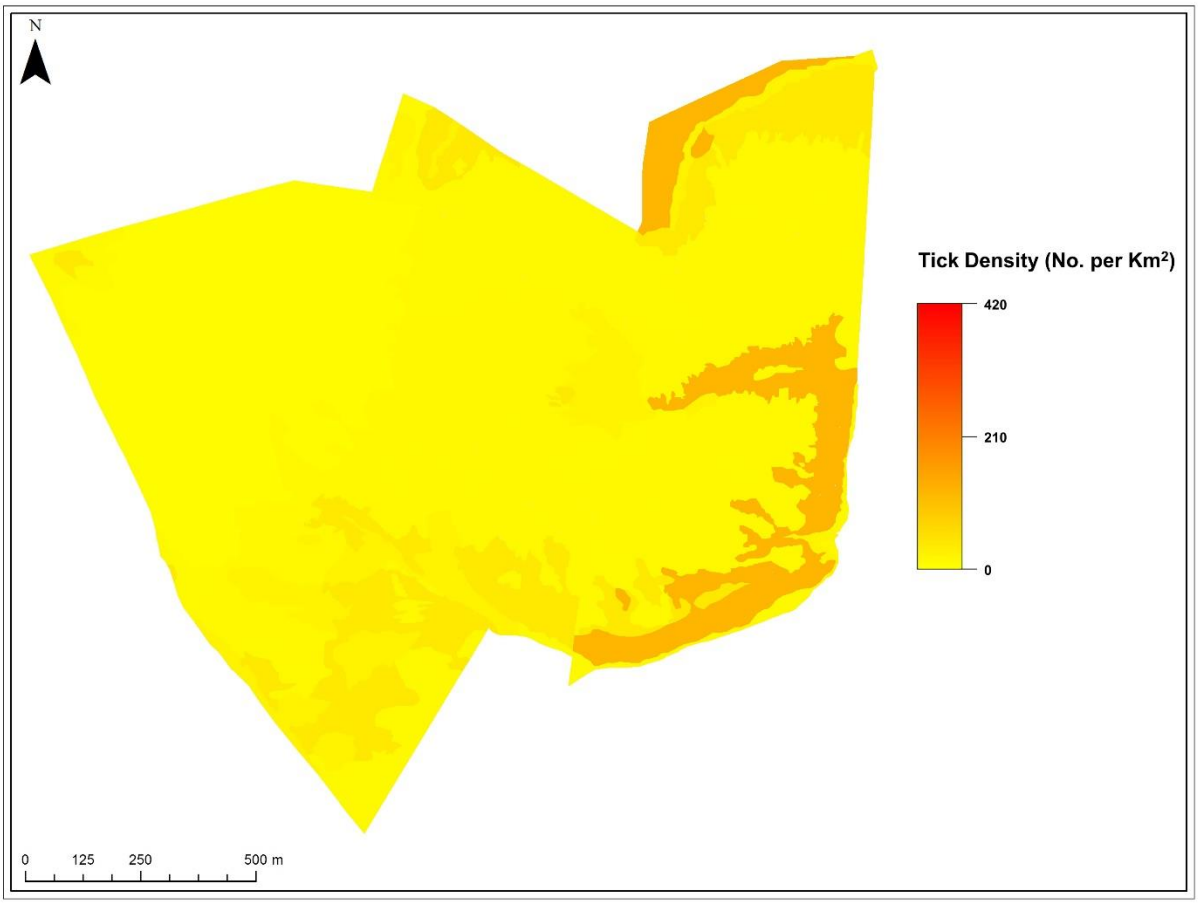


Figure 36: Map showing the estimated density of *Ixodes ricinus* in different parts of Squallacombe and Aclands based on the distribution of different habitats for 2015 (**A**) and 2016 (**B**).

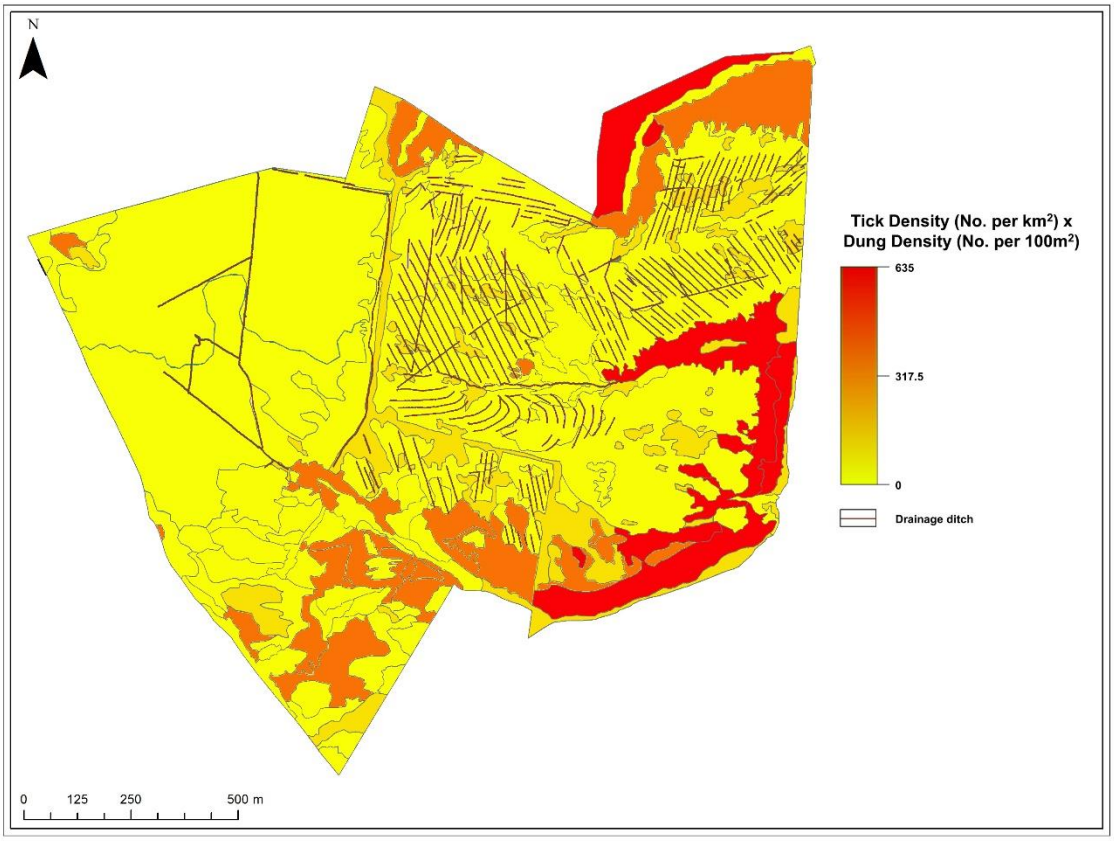


Figure 37: Map showing the estimated tick-borne disease risk in different parts of Squallacombe and Aclands, based on the distribution of different habitats. Disease risk is calculated by multiplying the density of *Ixodes ricinus* by the density of cattle dung density (from chapter 4).

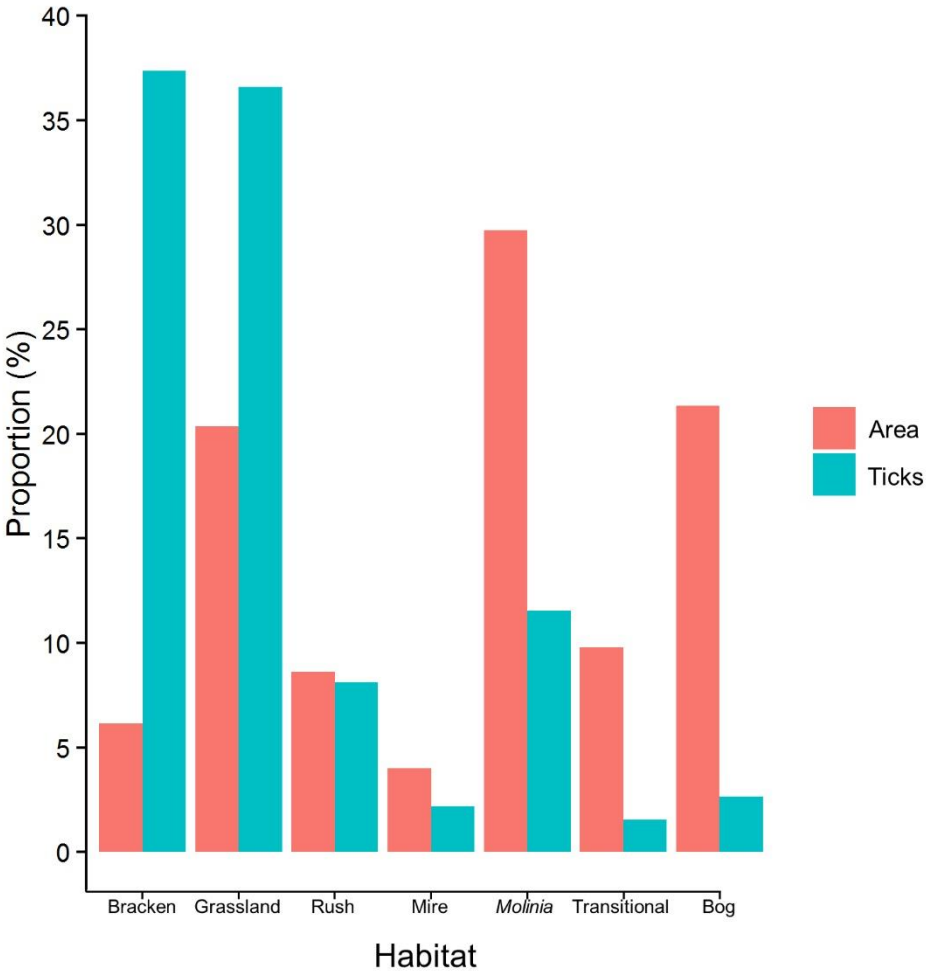


Figure 38: The contribution of each habitat type to the percentage of the total area surveyed, and the total number of ticks recorded. Based on a total area of 29312.74 m^2, and a total of 932 *Ixodes ricinus* individuals.

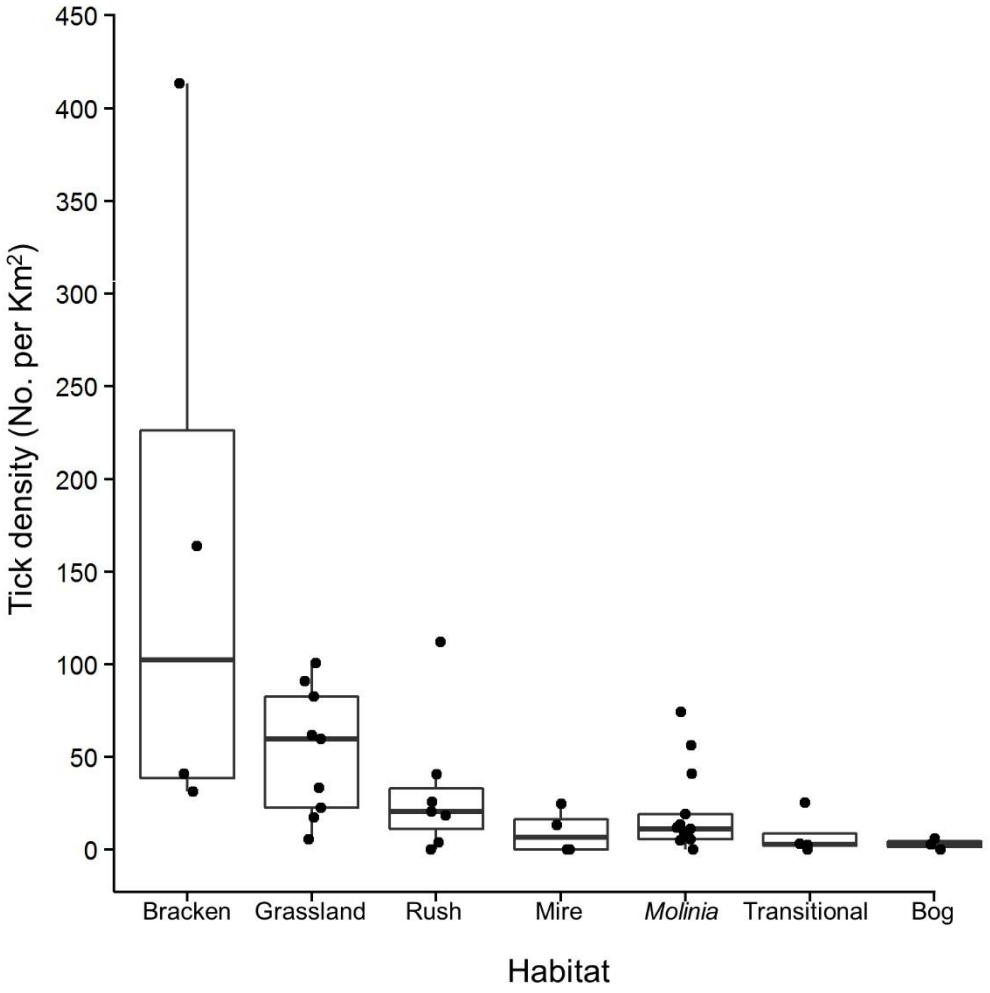


Figure 39: A comparison of the density of *Ixodes ricinus* in different habitat categories from surveys in the 2015 field season. Points represent the mean tick density in different vegetation communities, based on the combined results from all surveys of all sites. The centre line marks the mean value for tick density in each habitat category, and whiskers show the range, excluding outliers.

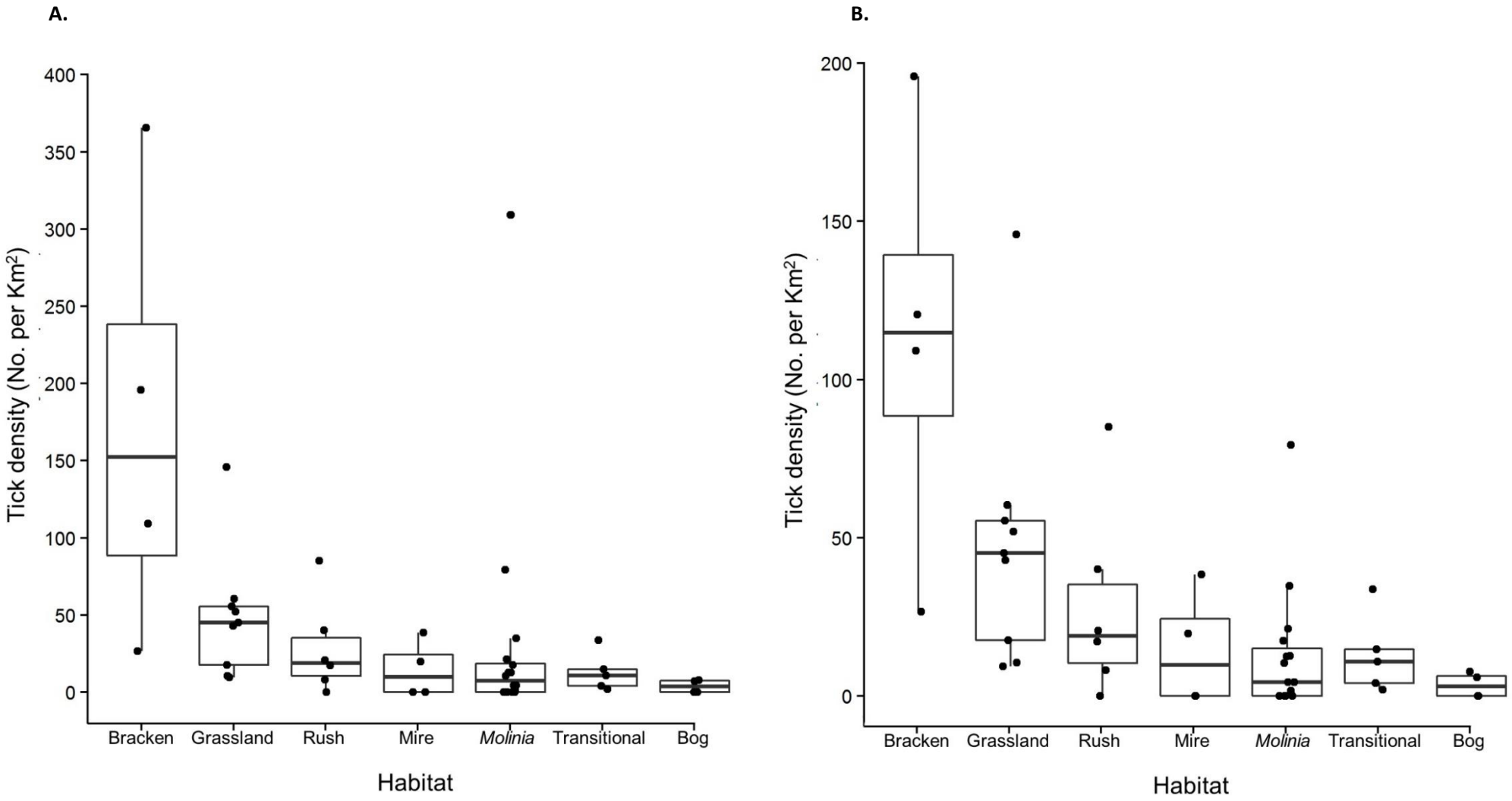


Figure 40: A comparison of the density of *Ixodes ricinus* in different habitat categories from surveys in the 2016 field season with the additional Squallacombe & Aclands survey included (**A**) and excluded (**B**). Points represent the mean tick density in different vegetation communities, based on the combined results from all surveys of all sites. The centre line marks the mean value for tick density in each habitat category, and whiskers show the range, excluding outliers.

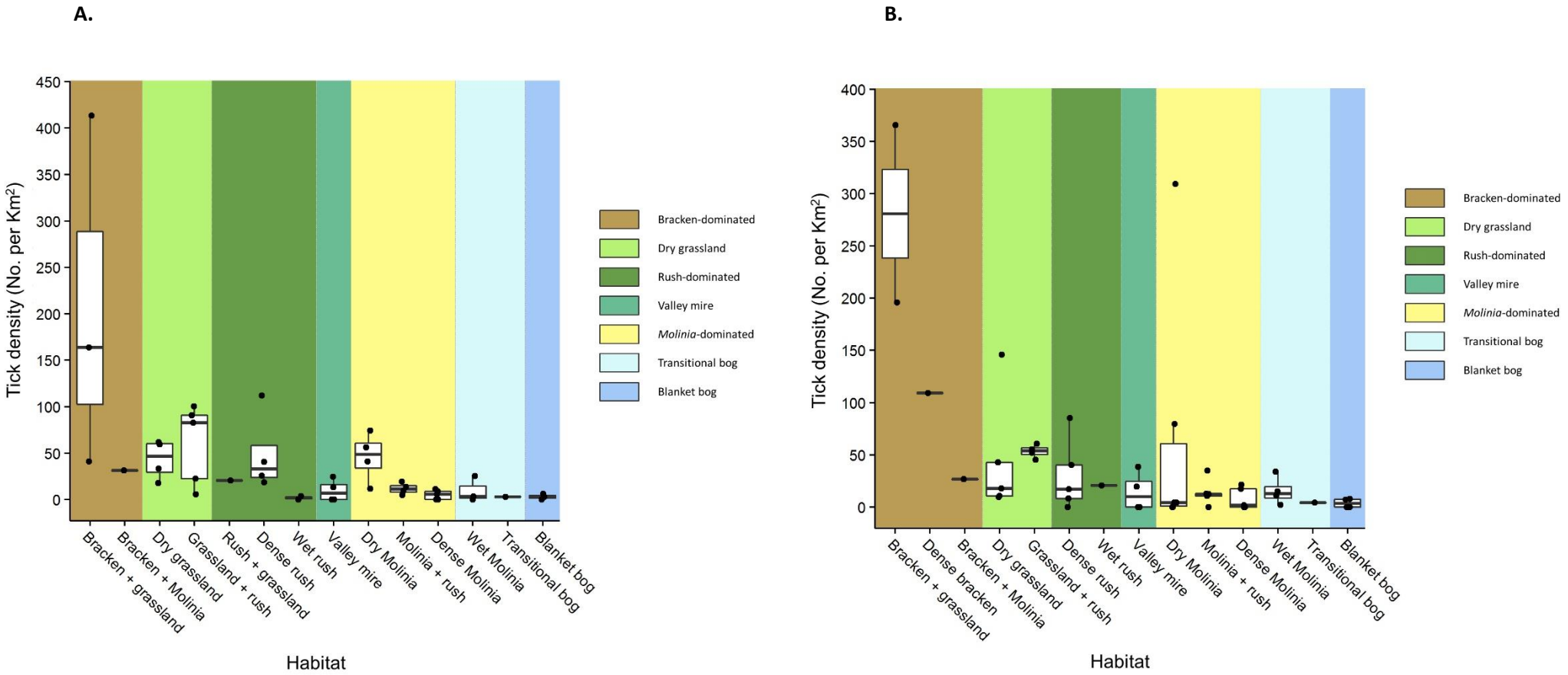


Figure 41: A comparison of the density of *Ixodes ricinus* in different habitat subcategories in 2015 (**A**) and 2016 (**B**). Points represent the mean tick density in different vegetation communities, based on the combined results from all surveys of all sites. The centre line marks the mean value for tick density in each habitat category, and whiskers show the range, excluding outliers.

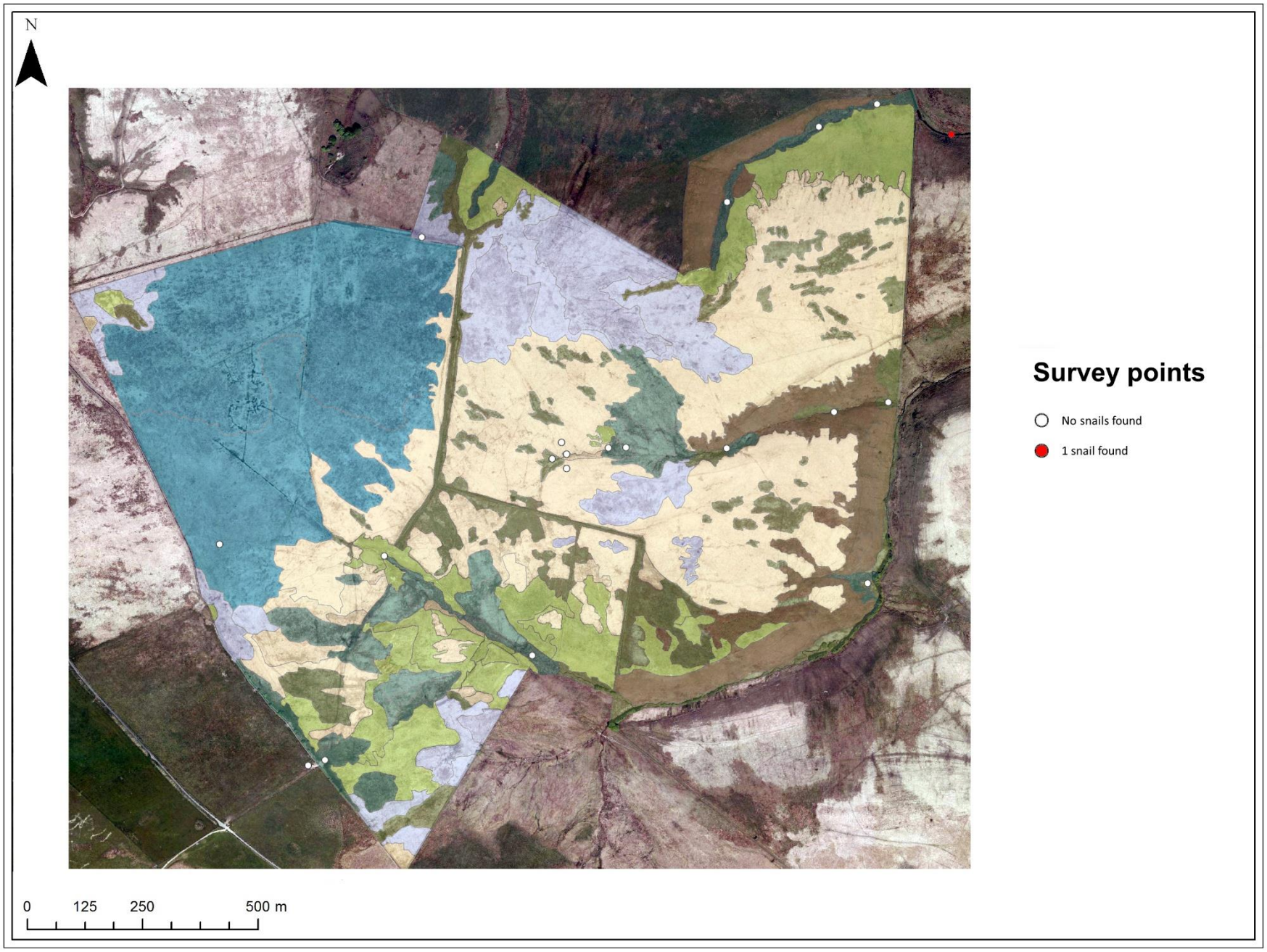


Figure 42: Map of locations searched for the presence of *Galba truncatula* at the Squallacombe and Aclands site. Habitat categories are overlaid, and described in Chapter 2.2.3.

5.3 Results

5.3.1 Ixodes ricinus

Overall, density of ticks was higher in 2015 than 2016 (Table 15). However, patterns at the site level varied, with Spooners and Hangley Cleave both recording slightly higher tick densities in 2016 than in 2015 (Table 15). At Squallacombe and Aclands differences in tick density between habitats were less pronounced in 2016 than in 2015 (Figure 36).

The proportion of the total area covered in each habitat type was not necessarily related to the proportion of the total number of ticks recorded in each habitat, with bracken-dominated and dry grassland habitats accounting for a disproportionately high number of ticks, and *Molinia*-dominated, transitional bog and blanket bog accounting for a disproportionately small number of ticks (Figure 37).

In 2015, density of ticks differed significantly between different habitat categories ($\chi^2_6 = 18.33$, $p = 0.0054$; Figure 38). In 2016, density of ticks differed significantly between different habitat categories both when the additional Squallacombe and Aclands survey was included ($\chi^2_6 = 17.8$, $p = 0.0067$; Figure 39) and when it was excluded ($\chi^2_6 = 19.77$, $p = 0.003$; Figure 39). There appeared to be differences between vegetation communities within habitat categories (Figure 40). There was no significant difference in tick density between pre- and post-restoration habitats ($\chi^2_1 = 1.7$, $p = 0.19$)

5.3.2 Galba truncatula

No individuals of *G. truncatula* were found within the site boundaries, but one empty shell was found close to the boundary of the Squallacombe and Aclands site (Figure 41).

5.4 Discussion

Ixodes ricinus and *Galba truncatula* populations in upland pastures

The results show that different moorland habitats differ in the densities of *I. ricinus* that they support. Bracken-dominated habitats supported the highest tick densities, followed by dry grassland habitats; indeed, these two habitat categories accounted for a very high proportion of the total number of ticks recorded despite making up a relatively low proportion of the total area surveyed. Within these habitat categories, bracken-dominated habitats appeared to support higher tick densities when in combination with patches of dry grassland, while dry-grassland dominated habitats generally supported higher densities when areas of soft rush were present.

These habitats share similar characteristics which could potentially explain their apparent higher densities of ticks. Vegetation cover appears to be an important factor in dictating the distribution of ticks in moorland pastures (Milne 1950a), and as the favoured habitats have high cover of tall vegetation this could be an important driver behind the higher tick densities they support. It is possible that the structure of these habitats might make them more favourable for ticks, with the presence of stands of taller, robust vegetation acting to provide shelter, both from wind and from high temperatures. High humidity is essential for tick survival (MacLeod 1934; MacLeod 1935; Milne 1950b), and the varied vegetation physiognomy of these communities may therefore help to provide suitable areas of higher humidity to reduce the risk of desiccation.

Aside from micro-habitat features, the high density of potential host species in these habitats could potentially be a driver behind the high abundance of ticks. Numerous studies have demonstrated the relationship between tick density and the distribution of host species such as deer (Jensen *et al.* 2000; Ruiz-Fons & Gilbert 2010; Qviller *et al.* 2016), and on the study sites livestock activity is greatest in areas of dry grassland, and is also high in areas of bracken (chapter 4.3.1), while red deer are also frequent in these areas. However, density of grazing animals does not appear to be the main driving factor behind density of ticks, as otherwise the largest populations might be expected to occur in areas of open dry grassland. The lower densities in dry grassland could be related to

the previously mentioned influence of habitat structure, with these vegetation communities resembling those of lowland pastures which are generally less suitable for ticks (Milne 1950a). Furthermore, it is possible that, while being favoured by large grazing animals, these habitats may support lower densities of other host species. Rodents are important hosts for *I. ricinus* nymphs, and grazing has been shown to reduce the abundance of small mammals in upland pastures (Evans *et al.* 2006), while studies in woodland have shown that decreased small mammal populations associated with cattle grazing can result in a reduction in tick abundance (Gassner *et al.* 2008). Therefore, it is possible that the high grazing pressure in open grassland habitat leads to the observed lower densities of *I. ricinus* by decreasing the abundance of small mammals. Overall, it appears that features of a habitat with a high density of *I. ricinus* are a combination of an abundance of host species, and stands of taller vegetation cover to provide shelter and facilitate questing.

High densities also appeared in the *Molinia*-dominated category in dry *Molinia* habitats. Dry *Molinia* habitats share some of the favourable characteristics of bracken-dominated and dry grassland habitats, with patches of grassland providing favourable grazing and *Molinia* tussocks acting as a substitute for bracken or soft rush to provide shelter and good questing sites. Therefore, it is possible that this habitat could pose a relatively higher threat than those wetter habitats consisting almost entirely of dense *Molinia* tussocks.

Patterns of tick distribution across different habitats were similar between survey years, although slightly weaker in 2016 due primarily to a drop in the density of ticks recorded in bracken-dominated habitats. Weather conditions in the seasons preceding periods of tick activity have a significant impact on abundance (Lauterbach *et al.* 2013; Berger *et al.* 2014), and it may be that differences between the two survey years are related to weather patterns. The summer of 2015 was cooler and wetter than average (Met Office 2017), which could potentially have affected tick survival and breeding, resulting in reduced numbers in 2016. Alternatively, the lower numbers could have been a result of the abnormally warm winter of 2015/16. When conditions are mild, tick activity may continue throughout the winter months (Dautel *et al.* 2008), and therefore it is possible that warm winter weather in 2015/16 may have encouraged ticks to

begin questing early, resulting in a protracted period of activity and weakening the typical spring population spike. Although the spring and summer of 2016 were not especially abnormal in terms of weather, surveys often had to be undertaken in conditions that were not ideal for tick activity, such as on breezy or cool and overcast days which may have reduced the number of questing ticks encountered.

Overall, the findings suggest that tick populationsare concentrated in particular habitats in moorland pastures. This could possibly be explained by the increased presence of livestock and other hosts in these habitats that tick densities are high; and the combination of large tick populations and heavy livestock use of these habitats could result in a higher threat of disease in these areas.

It would be desirable to carry out blanket drag surveys throughout the year, or at least from early spring through to late autumn, in order to determine whether differences in tick density between habitats remains consistent throughout the year. This would also provide a useful indication of tick phenology in the study area, thereby potentially helping to identify periods in which grazing animals are at greatest risk of coming into contact with *I. ricinus.* Furthermore, it would be valuable to carry out molecular studies on captured ticks in order to determine the prevalence of important pathogens, such as *Babesia divergens*, within these populations. While this study provides information on the spatial distribution of *I. ricinus* in upland pastures, an understanding of pathogen prevalence is important to determine how much of a risk to health these tick populations pose.

Surveys failed to find any individuals of *G. truncatula* on the study site, but one empty shell was located a short distance outside of the site boundary. The shell was located on a muddy bank in the upper reaches of the River Barle. At the point it was found, the river is larger and slower flowing than nearby streams which flow in to it from the moor. The location was at an altitude roughly 100 metres lower than the plateaus of the surrounding moorland. The habitat included some aquatic vegetation and algae of species that are absent from blanket bog and bog pools.

These findings could potentially support the absence of *G. truncatula* from peat soils, as suggested by Heppleston (1972). This would mean that, despite an abundance of wetland habitat, snails are absent from blanket bog and *Molinia*-dominated areas of moorland. It has been suggested that peat does not support the microalgal growth that the snails feed on, but it is possible that the more nutrient rich mud of the lower altitude streams and rivers may provide a suitable source of food.

Although no snails were found within the restoration area, they could potentially occur where suitable habitats are present. Habitats similar to that where the one shell was found are present on the small streams which flow off the moor. In places these form pools, with a suite of minerotrophic plant species which are notably different to the communities present in peatland habitats. These areas could potentially support snails, but as searches failed to locate any individuals it is likely that if present they occur at low density if at all.

Fasciolosis has been recorded in stock on the restoration sites (Hazel Kendall 2013 pers. comm.), but it remains unclear where animals are encountering the parasite. These findings suggest that animals are at low risk when grazing on moorland, but could perhaps face a higher risk of becoming infected when grazing lowland pastures close to water bodies. Nevertheless, there is some potential for animals to become infected with *F. hepatica* on moorland, and further work is required in order to determine whether populations are present in valley bottoms with slow-flowing, muddy streams which are similar to the favoured habitat of *G. truncatula* (Hourdin *et al.* 2006; De Roeck *et al.* 2014).

The effect of peatland restoration on vector/host populations

The results suggest that peatland restoration is unlikely to have a meaningful effect on parasite populations on moorland pastures, as comparison of pre- and post-restoration habitats shows no significant difference in parasite prevalence. Changes associated with restoration are likely to be concentrated in particular habitats, with an expected gradual switch from *Molinia*-dominated drier peatland to blanket bog communities (Haapalehto *et al.* 2010; Bellamy *et al.* 2011; D'Astous *et al.* 2013Menberu *et al.* 2016). Tick surveys show that *Molinia*-dominated, transitional bog and blanket bog habitats all support low densities of *I. ricinus*. An important factor behind the low tick population densities in wetter habitats is possibly the low use of these areas by wild or domestic grazing

animals, therefore limiting the number of potential tick hosts. Although some high tick densities were recorded in *Molinia*-dominated habitats, these were often in drier areas where patches of fine-leaved grasses may have encouraged greater use by herbivores. Differences in overwintering survival in different habitats have been reported in other *Ixodes* sp. (Lindsay *et al.* 1998), and this could potentially be another contributing factor for the observed differences in abundance between habitats.

It is possible that some of the ticks present in these habitats may have been brought in by hosts travelling from those areas supporting higher densities. Tick presence in an area can be reliant on the movement of host species (Estrada-Pena 2003), and ticks dropping off in to new habitats are only likely to develop permanent populations where conditions are favourable (Milne 1950a). Therefore, it is possible that tick populations in wetter habitats may vary year on year, with the presence and abundance of ticks being influenced by the movement of host species. Ticks might also breed in these wetter habitats, but due to the lower densities recorded it seems that this may occur less frequently than in drier areas.

Due to terrain, soil type and distance from drainage features, restoration is unlikely to alter the drier habitats favoured by *I. ricinus*. However, if rewetting were to reduce the area of these habitats, which could potentially occur where isolated patches are present among areas of drained peatland or at the boundary of peatland areas and dry grassland, then it is possible that disease risk on site would be reduced. Peatland restoration has been suggested as a means of reducing *I. ricinus* populations in afforested upland areas (Gilbert 2013), and on Exmoor a similar effect may occur if peatland habitats were to replace drier habitats such as rush and bracken-dominated pastures or dry grassland. While there is perhaps limited potential for this to occur on the sites studied, it could result in a reduced tick population where the distribution of habitats were to allow it to take place.

It would appear that peatland restoration is unlikely to affect the risk of Fasciolosis on Exmoor due to the unsuitability of the restored habitats for the host snail. *G. truncatula* may occur at low density in streams and pools in valley bottoms, but these habitats will not be significantly affected by restoration of

surrounding peatlands. Although peatland restoration is expected to raise the water table and increase the presence of standing water on sites, the resulting habitat will remain unsuitable for *G. truncatula* as peat is unfavourable as a substrate (Heppleston 1972). It is possible that rewetting could alter snail populations if local hydrology is affected, for example if flow rate of streams is altered. However, the potential effects of this would be hard to predict, and would require study of the effects of peatland rewetting on nearby water bodies present immediately downstream.

Overall, peatland restoration should not necessarily be expected to have a significant impact on the risk of tick-borne disease or Fasciolosis on moorland pastures as both pre- and post-restoration habitats have similarly low populations of vector/host species.

Conclusion

Ecosystem change has potential to affect populations of vectors and parasites. Changes in land use have produced favourable conditions for vectors and pathogens, resulting in disease outbreaks and emergence. In addition, changes in climate may increase the spread of disease and allow the distribution of vectors to expand. Aside from the threat to human health, the potential for infectious disease to affect agriculture is of great importance. Where disease results in loss of livestock or crops the results may be severe, with potential for food shortages and economic damage. The distribution of vectors and pathogens within a landscape is often aggregated based on fine-scale habitat preferences. Thus, parasite populations can show great variation at extremely small spatial scales. As a result, a small change in habitat could potentially lead to a large change in the threat of disease in an area. It is therefore crucial that we understand the fine-scale distribution of vectors and parasites in order to allow us to predict how ecosystem change may affect their populations. With an understanding of the distribution of disease risk, it may be possible to take preventive measures to reduce the chances of infection.

It has been suggested that habitat degradation may improve conditions for the spread of disease. Initiatives are increasingly aiming to restore degraded habitats to their former state for reasons of conservation or ecosystem service provision. The effect of habitat restoration is likely to be highly variable; complex, functioning ecosystems may reduce disease pressure on human populations by providing a diversity of alternative hosts and reducing the prevalence of simplified habitats favourable for breeding of vectors. However, as conservation schemes may result in increases in the populations of wild host species, they could provide a reservoir for pathogens and increase the risk of humans coming in to contact with disease. This study highlights the fact that management techniques, in this case agricultural improvement, may unintentionally improve conditions for vectors and hosts, thereby increasing disease risk. In such cases, if habitat restoration were to decrease the area of such high-risk habitats, it could lead to a reduction in the incidence of diseases of concern to humans and livestock.

Chapter 6: Thesis discussion

6.1 Agricultural productivity in upland pastures

This study has provided a framework for assessing the agricultural productivity of semi-natural pastures. A number of factors contribute to the productivity of a pasture, and therefore a number of factors need to be evaluated in order to obtain an accurate estimate of productivity. Extensive pastures are not uniform; typically they will comprise a number of different habitat types and vegetation communities. In some cases, the difference may be as clear-cut as forest versus grassland, but even in rough grassland pastures there will be differences in the distribution of different vegetation types. In attempting to assess the grazing value of different habitats it is important to examine factors that are likely to make the most significant contributions to productivity. Factors such as nutritional quality of the sward, and habitat preferences of grazing animals will have a direct impact on productivity (Duble *et al.* 1971; Mayombo *et al.* 1997; Gleghorn *et al.* 2004; Boland *et al.* 2013). If sward quality is too low then grazing will not be profitable, with animals losing condition rather than gaining weight (Grant *et al.* 1987; Beauchemin 1991; Munoz *et al.* 2016). However, the results of this study demonstrate that even if grazing land produces a sward with relatively good nutritional quality, if it is unpalatable or just unfavourable to livestock its value will be diminished. In addition, other factors such as disease risk will make a major contribution to the productivity of a pasture, with parasitic and vector-borne disease resulting in major economic losses (Defra 2002; Mitchell 2002; Minjauw & Mcleod 2003; Zintl *et al.* 2003; Kivaria 2005; Pritchard *et al.* 2005; Knubben-Schweizer *et al.* 2010; Skuce & Zadoks 2013). Measures such as these need to be considered in combination, and the results of this work suggest that different factors may act either synergistically or antagonistically; thus the value of a pasture can only be estimated when a number of different variables have been considered.

The variables studied here are by no means exhaustive, and in other farming systems ecosystem change could affect productivity in a number of ways; for example, the provision of valuable services such as pollination or biological pest

control may be altered (Klein *et al.* 2007; Bommarco *et al.* 2013). As a result, the more factors that may be considered in an assessment, the more accurate it is likely to be. The results of this study demonstrate that the productivity of upland pastures is spatially variable and dependent on the distribution of different habitat types. The study examined three different measures of productivity: sward quality, livestock grazing behaviour, and parasite prevalence. The results suggest that these different measures are not independent of one another, and all are likely interact to some degree. Studies suggest that nutritional quality is important in dictating cattle diet selection (Kingery *et al.* 1996; Lamoot *et al.* 2005; Putfarken *et al.* 2008), and therefore it may have been expected that the quality of the sward would dictate livestock grazing preferences. However, when taking the sward as a whole this does not appear to be the case, as the results suggest that nutritional quality is relatively uniform between habitats, and therefore should not account for the significant differences in levels of cattle grazing. Where vegetation structure allows, cattle will select favourable forage from within a habitat (France *et al.* 2008; Samuels *et al.* 2014), and therefore although this study found the sward as a whole to be fairly uniform in terms of quality, cattle may have been able to selectively feed within certain habitats to obtain a reasonably high quality diet.

Further research would be of value to establish diet composition of cattle on these pastures in order to determine which species are being selected. While it is possible to speculate based on the percentage cover of different species in different habitats, it would be of interest to gain an actual measure of diet composition, as this may help to explain different levels of grazing in different habitats.

The interaction between nutritional quality and grazing level is likely to work both ways, as grazing by livestock has the potential to alter the quality of a sward. Indeed, it has been suggested that the maintenance of productive, semi-improved grass lawns in uplands is dependent on grazing activity (Hulme *et al.* 1999). There may be a number of different means by which this is achieved: plant species composition may be altered, with poor-quality species prevented from establishing; fresh, higher quality regrowth may be encouraged by grazing; and animal excreta may add nutrients to the soil resulting in a higher quality and

volume of forage. As a result, favoured grazing habitats may, at least in part, remain favourable due to the higher levels of grazing that they receive.

The effect of grazing on ecosystem structure may also have an effect on the abundance and distribution of arthropod vectors such as ticks (Milne 1950a; Gassner *et al.* 2008; Steigedal *et al.* 2013). As tick density differsbetween particular habitat types (Estrada-Pena 2001; Wielinga *et al.* 2006; Medlock *et al.* 2008; Tack *et al.* 2012a; Tack *et al.* 2012b; Ceballos *et al.* 2014;), changes in vegetation composition and structure driven by grazing would have the potential to affect their distribution. The results of this study show tick abundance to be greatest in areas of variable vegetation height, where short swards are interspersed with stands of taller vegetation. Taller stands may benefit ticks by acting as good questing sites, and providing shelter from high winds and temperatures. Furthermore, wild hosts may be concentrated in such areas as the vegetation provides good breeding conditions for rodents, and cover for grazers such as deer to rest in. As a result, livestock grazing may have a mixed impact on tick abundance. If grazing were to prevent the establishment of taller stands of vegetation and maintain homogeneous short swards, then the abundance of ticks might be suppressed. However, the presence of grazing livestock means that additional hosts are available for ticks, and therefore abundance may increase. Indeed, there appears to be some overlap between habitats supporting the highest densities of ticks and those receiving the highest levels of use by livestock. Overall, habitats with the highest tick-borne disease risk are those that provide a combination of taller vegetation, for shelter, and shorter vegetation, to attract host grazers, and it is likely that grazing by livestock contributes to the maintenance of such habitats (Hulme *et al.* 1999).

While these findings provide an indication of differences in the populations of *I. ricinus* in upland habitats, further study would be valuable. Tick abundance varies significantly between habitats; however, it would be beneficial to obtain a measure of the infection rate of different pathogens of interest within the tick population, as this can be variable (Halos *et al.* 2010; Hamsikova *et al.* 2016; Millins *et al.* 2016). This would provide a better indication of the risk of infection in livestock, and allow more accurate mapping of disease risk if infection rates within ticks were found to be spatially variable. Furthermore, while this study

examined the prevalence of two vector species of regional significance, *Ixodes ricinus* and *Galba truncatula*, other parasites and vectors contribute to disease risk in upland pastures. For example, further studies on the distribution and vector competency of *Culicoides* midges in upland pastures may provide an indication of future risk of outbreaks of diseases such as Schmallenberg and bluetongue virus (Wittman & Baylis 2000; Tarlington *et al.* 2012).

These findings highlight the impact of past and present management practices on the productivity of semi-natural upland pastures. The vegetation communities of British uplands have been heavily shaped by human land use (Copeman 1978; Miles 1987;Maltby 1995; Holden *et al.* 2007). Indeed, the open character of uplands is entirely due to human activity, with the landscape previously being covered in forest (King 1977; Averis *et al.* 2004). However, the potential to revert to this state is likely to be limited due to the extent of change since deforestation occurred, with infertile and unstable soils, combined with large populations of wild and domestic herbivores working to inhibit tree regeneration in uplands (King 1977; Copeman 1978; Maltby 1995; Clutton-Brock *et al.* 2004). The fine-scale distribution of different vegetation communities in modern, open landscapes of uplands are also shaped by human activity. Processes such as vegetation clearance, grazing, drainage, burning, ploughing, fertilisation, liming and seeding have acted to change the vegetation of upland landscapes (Miles 1987; Maltby 1995).

This study demonstrates that, in terms of grazing, it appears that the most productive habitats on Exmoor are those that have been most heavily improved. Areas which have been ploughed, limed, and reseeded have produced lawns of minerotrophic grass species which appear to provide relatively favourable grazing, and the majority of livestock activity was found to be concentrated in such habitats. It is difficult to determine how persistent these habitats are, and how much management would be required to maintain them: grazing is likely to be necessary to prevent invasion by more robust grass species, and the plant community may change to one more characteristic of acidic soil over a longer time scale (Hulme *et al.* 1999). While this demonstrates that improvement techniques have been effective in increasing productivity in these upland pastures, it also highlights the difficulty of farming in marginal areas. The results

show that productive areas have required the most intensive management in order to create land of a reasonable quality for grazing, while in other habitats interventions such as drainage have failed to produce productive land. As suggested elsewhere (Wilson *et al.* 2010), drainage of peatland has failed to produce swards which are favourable for grazing, instead resulting in extensive *Molinia*-dominated pastures which are seldom used by livestock. In addition, where improvement is effective, it may also have unexpected negative consequences. In the case of Exmoor, some of the more productive grazing areas have the highest densities of ticks; as a result, while a habitat may provide high-quality grazing there may be trade-offs, with an increased risk of animals encountering disease vectors when grazing these areas. While minerotrophic grassland provides favourable grazing, the extent to which this habitat could be created is limited by the physical characteristics of upland landscape. The creation and maintenance of such grasslands would be costly, and likely to be limited to areas with suitable topography and soil type (Miles 1987; Hulme 1999); it is constraints such as these which qualify upland pastures as Less Favoured Areas, with farming in such areas recognised as being marginal (FERA 2015).

Upland areas of the UK share a number of similar characteristics, and a similar suite of vegetation communities may exist in widely separated areas (Averis *et al.* 2004). While the climate of Exmoor may be considerably more favourable than other UK uplands (Miller *et al.* 1984) it is possible that the findings of this study are applicable to upland areas elsewhere in the UK where similar habitat types are present. However, further research would be necessary to confirm that this is the case, and also to establish the agricultural value of upland habitats that were not examined in this study. For example, heather moorland is an important and common habitat in other upland areas, particularly northern England and Scotland (Holden *et al.* 2007; Worrall *et al.* 2007), but it covers a relatively small area of Exmoor, and therefore was not included in the current study. Furthermore, tree cover is occasionally present in some upland areas in the form of plantations, or the presence of deciduous trees on sheltered valley sides (Averis *et al.* 2004; Mount *et al.* 2005). Although perhaps unlikely to affect grazing quality, tree cover could alter disease risk by providing favourable habitat for host species and thereby increasing the abundance, or altering the

spatial distribution of ticks (Boyard *et al.* 2011; Dobson *et al.* 2011; Kiewra *et al.* 2017).

6.2 The effect of peatland restoration on agricultural productivity

This study potentially suggests that, overall, rewetting of peatlands on grazing land may have a minimal impact on productivity. The results suggest that blanket bog communities of pristine peatland are not favoured for grazing; however, drainage appears to be ineffective as a means of converting blanket bog in to favourable grazing land, instead producing *Molinia*-dominated pastures which were also rarely used by livestock. Perhaps as a consequence of the low levels of livestock grazing, tick-borne disease risk also appears to be low, with both pre- and post-restoration habitats supporting low tick densities. As livestock distribution is affected by terrain (Sheath 1983; Kaufmann *et al.* 2013), it is possible that on Exmoor livestock movement could be affected if restoration were to increase due to the area of standing water and boggy ground. However, the findings of the study show that both pre- and post-restoration habitats are occasionally visited by livestock, so it appears that animals are able to transit through the habitats when necessary. Each habitat could potentially offer minor advantages over the other. The results of the sward quality analysis suggest that *Molinia*-dominated pastures appear to provide a reasonable quality of grazing when there is fresh growth in the early summer, while blanket bog may provide grazing later in the year, when the quality of *Molinia* has declined, due to the high cover of dwarf shrubs. Overall, however, it appears that neither habitat makes a significant contribution to agricultural productivity in a typical mosaic of upland vegetation types.

While these findings should apply to other peatland areas, the impact of peatland restoration would depend on characteristics of the site being restored, and in particular the availability of other vegetation types. As previous studies have suggested that cattle typically avoid blanket bog communities (Grant *et al.*

1987), it is possible that if pre- and post-restoration habitats were compared in isolation by grazing livestock in a pasture consisting of only those habitats, a stronger difference in grazing value may emerge. However, certain upland sward types are recognised as being unsuitable for grazing due to unacceptably low levels of animal performance (Grant *et al.* 1987; Common *et al.* 1994), and it is likely that grazing cattle on *Molinia* pasture and blanket bog alone would not be sustainable in the long term.

The effects of peatland restoration are spatially and temporally variable. On the study sites, restoration has resulted in relatively small changes thus far, with vegetation patterns apparently relating to fine-scale variations in the depth of the water table associated with drainage features (Gatis *et al.* 2016). However, restoration projects elsewhere have resulted in significant increases in blanket bog vegetation (Komulainen *et al.* 1999;Tuittila *et al.* 2000; Haapalehto *et al.* 2010; D'Astous *et al.* 2013; Menberu *et al.* 2016), and it is anticipated that further study over longer timescales will demonstrate the extent to which peatlands on Exmoor can be expected to change following restoration. In the short term, peatland restoration is unlikely to have an effect on the more productive habitats of Exmoor, as rewetting will affect drained, *Molinia*-dominated areas. However, if over longer timescales peatland restoration were to change the extent of productive habitats such as minerotrophic grassland, agricultural productivity could be affected. This could plausibly happen in certain situations, such as where patches of grassland are present among areas of drained peatland, or where areas of grassland border areas of peatland. In these cases, it is possible that rewetting could eventually lead to encroachment of *Molinia* and bog plants at habitat boundaries, which would decrease the area of favourable grazing on a site. Again, this is likely to be highly situation dependent, and therefore localised; where grasslands exist on well-drained steep slopes it is unlikely that peatland restoration will have any effect. However, while findings from the sites studied in this project suggest that peatland restoration will have a limited impact on productivity, the effect could perhaps be more profound in circumstances where rewetting would lead to a decrease in the area of favoured grazing habitats.

These findings could have important implications for the Exe catchment. The Exe supplies water to over 220,000 people (Reid 2010), but the region has had problems with flooding in recent years and yet, ensuring a reliable water supply during periods of low rainfall has proven logistically difficult and costly (Grand-Clement *et al.* 2014; Luscombe *et al.* 2016). One of the key aims of the Exmoor Mires Project is to alter the flow of water from the head of the catchment by rewetting peatlands at the source of the Exe, thereby improving the quality of water entering the river and reducing water treatment costs. However, as Exmoor's peatlands are typically used for grazing there has been potential for rewetting to conflict with existing land uses. The results of this study suggest that peatland restoration need not necessarily be detrimental to agriculture whilst improving water quality on Exmoor. Furthermore, by obtaining estimates of the agricultural value of different vegetation communities, it might be possible to predict how the productivity of these sites will change in future if further habitat changes occur over time.

While this study has examined a number of important factors, these are not the sole contributors to the agricultural productivity of a site. If peatland restoration were to make sites harder to access for farm workers, due to increased wetness and areas of standing water, this would make it more difficult to carry out essential tasks. If this increases the time spent by farm workers surveying a pasture then there will be an economic cost; it may be more difficult to access injured animals, move herds between areas, and place supplementary feeds. The effects of problems such as these are likely to be site specific, varying depending on factors such as topography and distribution of different habitats. Thus, while a habitat-based approach can provide an estimate of a pasture's productivity, the circumstances at individual sites should be considered when determining the way in which habitat change might affect grazing.

While this study may provide an indication of habitat-based variability in the agricultural productivity of upland pastures, it has limitations. The data collection was temporally and spatially restricted, and in order to confirm how consistent these results are it would be valuable to carry out similar surveys in a number of different years across a number of different regions. A habitat-based approach to estimating spatial variability in agricultural productivity could potentially be a

valuable tool, but further work is required in order to test the reliability of the technique.

6.3 Ecosystem change

Human land use can change ecosystems, and a large portion of the global land surface has been modified by human activity (Vitousek *et al.* 1997; Butchart *et al.* 2010; Ellis 2011; Pereira *et al.* 2012). Human driven ecosystem change is often carried out for reasons of improving the land for various uses, with agriculture being one of the most significant (Matson *et al.* 1997; Tilman *et al.* 2001; Green *et al.* 2005).

Numerous different means may be employed to increase the suitability of an ecosystem for agriculture: forest clearance to create pastures; artificial fertilisation to increase grazing quality; and elimination of wild predators to protect livestock. However, changes such as these can have an impact on the structure and function of the modified ecosystem and those around it (Scanlon *et al.* 2007; Blann *et al.* 2009; Stoate *et al.* 2009; Laurance *et al.* 2014). While there may be immediate benefits to such management techniques, there may also be unintended negative consequences (Tilman 1999; Bilotta *et al.*2007; Brazier *et al.* 2007; Dale & Polasky 2007). Soil disturbance may result in a loss of soil and a reduction in soil stability, decreasing the potential to use the land for agriculture (Diacono & Montemurro 2010; D'Odorico *et al.* 2013). Addition of nutrients may lead to eutrophication of nearby water bodies (Tilman 1999; Gordon *et al.* 2008) decreasing the quality of the available water. Loss of wild predators may result in trophic cascades, with changes in the abundance of species at lower trophic levels (Daskalov 2002; Hebblewhite *et al.* 2005; Estes *et al.* 2011). Upland pastures provide an example of the unintended consequences of human intervention, with deforestation leading to the creation of large areas of unproductive, infertile grazing land. Even when attempted at finer scales improvement may have a negative effect, with the results of this study demonstrating that the generation of fertile pasture land may lead to the localised abundance of parasites due to the concentration of host grazing species it attracts.

Land conversion may be responsible for the erosion of ecosystem services (Nasi *et al.* 2002; Foley *et al.* 2005). Intact ecosystems provide a number of services of high value to humans such as water regulation, disturbance regulation, and crop pollination (Diaz *et al.* 2006; Guo *et al.* 2010; Costanza *et al.* 2014). However, where the structural complexity of an ecosystem is lost, key processes may also disappear resulting in a decrease in the quantity of services provided (Isbell *et al.* 2011). Due to the difficulty of estimating the value of regulatory and supporting ecosystem services (Costanza *et al.* 1997) they may be overlooked as humans attempt to obtain more easily quantifiable goods and services.

However, as the value of ecosystem services is increasingly recognised, the number of schemes attempting to restore ecosystem function is increasing (Aronson *et al.* 2006). Restoration may be passive or active, but in either case aims for the conversion of a degraded ecosystem to a former state (Lavoie & Rochefort 1995; Kollmann & Rasmussen 2012; Gonzalez *et al.* 2014). The success of such projects is variable (Benayas *et al.* 2009), but there are a number of examples of ecosystems regaining some former function after damaging processes are halted, or restoration techniques are employed (Koch & Hobbs 2007; Jenkins *et al.* 2010). In some cases restored ecosystems may never regain the full functionality of pristine ecosystems (Benayas *et al.* 2009; Bullock *et al.* 2009), but it is likely that they will offer some improvement in service provision over those that are heavily degraded (Hilderbrand *et al.* 2005; Haigh 2006; Wilson *et al.* 2010; Waddington & Price 2013).

Although potentially beneficial, restoration ecology can cause conflict as the goals of restoration projects may appear incompatible with existing land uses. The effects of restoration on humans may also be highly asymmetrical in nature; if restoration work is detrimental to a landowner, losses will be concentrated on an individual, while benefits, in the form of ecosystem services, will be shared among the wider population. As a result, the effects of a restoration project need to be considered carefully in order to minimise any negative impacts on humans and their livelihoods. However, this study demonstrates that restoration cannot be assumed to be detrimental to the existing land use, as converted ecosystems may not necessarily be performing their intended purpose efficiently.

6.4 Conclusions

This study examines the productivity of different upland habitats in order to determine how ecosystem change has affected current agricultural productivity, and how it might affect productivity in the future. The findings demonstrate that spatial variability in the agricultural productivity of upland pastures is driven by the distribution of different habitat types, and if future environmental change were to result in changes in ecosystem structure then productivity could be further affected.

This study could potentially provide an example of a case where restoring an ecosystem will not have a negative effect on existing land uses. The restoration of peatlands has the potential to provide numerous ecosystem services of great value to large numbers of people, without being detrimental to those people whose livelihoods are directly affected by the peatlands as they are, in their current, degraded state. Furthermore, this work highlights the possibility of determining the effect of restoration on components of an ecosystem by using a habitat-based approach to predict the way in which important factors may change as an ecosystem reverts to its former state.

The findings highlight the potential for environmental change to affect ecosystem structure. Change in vegetation communities is indicative of changes in abiotic and biotic processes, and such change will affect a number of other ecosystem characteristics. Vegetation structure influences the distribution and abundance of different animal species, but it will also affect human land use. While human land use is a key driver of vegetation change, the resulting vegetation communities will dictate what the land may be used for, and how efficiently a chosen land use may be carried out. As a result, past changes in vegetation communities have had a profound impact on ecosystem structure and function, and human land use, and these will continue to be affected by future environmental change.

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Appendix 1

Summary tables of recorded values of different sward quality measures obtained during a pilot study between 2012 and 2015. The study is described in Chapter 3.2.1.

% Dry Matter

Transect	Autumn 2012	Spring 2013	Autumn 2013	Spring 2014	Summer 2014	Autumn 2015
Aclands 1	41.8	38.17	35	34.8	38.15	43.9
Aclands 2	40.6	42.12	47.3	35.27	36.87	43.77
Aclands 3	40.38	43.02	33	33.43	36.83	44.37
Aclands 4	37.05	38.2	38	32.15	36.95	40.77
Aclands 5	36.8	39.2	38.9	32.13	37.42	41.4
Aclands 6	36.47	36.8	44.2	33.62	38.17	42.4
Spooners 1	30.05	37.93	39.77	31.8	32.7	39.93
Spooners 2	27.78	38.1	38.63	33	34.1	38.93
Spooners 3	26.37	36.72	42.5	31.7	32.2	39.83
Spooners 4	27.13	40.58	38.08	32.4	31.6	40.67
Spooners 5	39.68	37.08	40.25	31.2	30.3	38.23
Spooners 6	39.05	36.78	41.88	32.2	31.9	40.13

% Neutral detergent fibre

Transect	Autumn 2012	Spring 2013	Autumn 2013	Spring 2014	Summer 2014	Autumn 2014
Aclands 1	59.67	52	66.8	53.4	56.33	62.3
Aclands 2	77.5	53.48	65.9	55.25	58.28	63.27
Aclands 3	62.68	59.25	78.2	55.37	57.93	62.2
Aclands 4	69.22	54.8	71.8	52.98	56.33	59.53
Aclands 5	69.88	55.77	74.9	55.53	59.27	57.5
Aclands 6	71.77	52.43	68.8	54.07	57.27	58.3
Spooners 1	62.38	54.37	67.53	55.6	60.2	56.77
Spooners 2	61.88	52.08	66.28	53.7	57.5	60.97
Spooners 3	65.75	55.03	66	52	59.7	58.03
Spooners 4	65.98	59.73	66.08	51.7	60.3	56.7
Spooners 5	64.05	55.45	66.32	49.8	62.8	55.2
Spooners 6	65.15	55.12	65.33	53.9	58.1	63.87

% Digestibility

Transect	Autumn 2012	Spring 2013	Autumn 2013	Spring 2014	Summer 2014	Autumn 2014

Aclands 1	60.5	62.5	57	63	61.33	59.43
Aclands 2	67.33	61.83	55	62.17	60	58.33
Aclands 3	59.5	59.17	57	62.5	61.5	59.47
Aclands 4	65	61.5	56	63.17	61.33	59.93
Aclands 5	56.83	60.5	56	62	60.83	61.67
Aclands 6	63.83	63.17	57	62.83	61.17	61.73
Spooners 1	61.83	63.17	58	63	60	61.87
Spooners 2	61.5	63.17	57.83	64	61	61.3
Spooners 3	60	61.17	58.33	64	60	61.17
Spooners 4	60.67	58	57.83	64	59	62.4
Spooners 5	58.5	61.33	58.33	65	60	62.77
Spooners 6	58.17	61.67	58.83	63	61	60.17

Metabolisable energy (KJ/g)

Transect	Autumn 2012	Spring 2013	Autumn 2013	Spring 2014	Summer 2014	Autumn 2014
Aclands 1	9.52	9.87	9	9.92	9.6	9.37
Aclands 2	10.58	9.68	8.7	9.77	9.45	9.17
Aclands 3	9.37	9.27	9	9.85	9.65	9.33
Aclands 4	10.2	9.65	8.8	9.92	9.6	9.4
Aclands 5	8.97	9.52	8.8	9.75	9.57	9.67
Aclands 6	10.03	9.93	8.9	9.9	9.57	9.7
Spooners 1	9.72	9.9	9.12	9.9	9.5	9.7
Spooners 2	9.63	9.9	9.05	10	9.5	9.6
Spooners 3	9.43	9.57	9.15	10	9.5	9.57
Spooners 4	9.5	9.08	9.08	10.1	9.3	9.77
Spooners 5	9.18	9.65	9.1	10.1	9.4	9.87
Spooners 6	9.17	9.67	9.27	9.9	9.5	9.47

% Crude protein

Transect	Autumn 2012	Spring 2013	Autumn 2013	Spring 2014	Summer 2014	Autumn 2014
Aclands 1	13.17	14.42	11.2	18.85	15.78	9.8
Aclands 2	14.75	14.8	12.4	18.43	14.43	10.27
Aclands 3	14.25	13.85	12	21.65	16.72	10.73
Aclands 4	17.1	17.7	11.8	23.12	16.87	13.57
Aclands 5	12.68	16	11.3	20.9	15.77	13.23
Aclands 6	17.43	18.45	13.9	21.3	15.7	12.1
Spooners 1	15.03	17.42	13.5	20.8	15.6	11.63
Spooners 2	16.35	17.37	14.25	19.6	16.8	13.33
Spooners 3	15.02	14.6	12.78	19.5	16.5	12
Spooners 4	13.98	15.4	14.15	20.3	16.3	13
Spooners 5	13.88	18.05	13.8	19.7	15.9	13.4
Spooners 6	13.57	17.2	13.47	20.1	18.3	11.7